# THE CONSEQUENCES OF *LIGUSTRUM SINENSE* (CHINESE PRIVET) INVASION OF PIEDMONT FLOODPLAIN FORESTS IN SOUTH CAROLINA: EFFECTS ON PLANT SPECIES AND FACTORS INFLUENCING DISTRIBUTION.

A Thesis

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Master's of Science

by

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ABSTRACT

Invasive species and human land use are related global change drivers that can confound interpretations of native plant declines. Invasive plant species are reported to negatively affect native plant species, but recent research questioned the interpretation that invasive plants are the sole cause of native plant species decline. At the same time human land use has resulted in direct and indirect changes to habitat and disturbance regimes. Riparian habitats are closely associated with human dominated systems and changes to the natural flow regime have been observed with development. In the southeastern United States floodplain forests are being rapidly invaded by *Ligustrum sinense* (Chinese Privet) a non-native shrub and provide a model system to investigate mechanisms driving invasive species dynamics. This study examined (1) if *L. sinense* is the direct cause of native plant decline and (2) what factors influence its distribution across the landscape.

This project used both observational and experimental designs to investigate the effect of *L. sinense* on plant species. I conducted a vegetation survey of twelve floodplain forests in the Piedmont ecoregion of South Carolina. Additionally, at one site an experiment was conducted for two growing seasons (63 weeks) to compare the growth and survival of native plants under mature *L. sinense* stands. Results of the vegetation survey show that sites with mature *L. sinense* had significantly lower herbaceous plant cover, total plant abundance, and native species richness. At the local level results from the transplant experiment show drastic effects of *L. sinense* on native plant seedlings with both decreased survival and growth. The parallel results of landscape and local scales reveal that *L. sinense* is a cause of native species decline. Invasion of *L. sinense* inhibits the herbaceous understory and prevents the regeneration of canopy trees by suppressing seedlings. This research supports the hypothesis that certain

invasive plants can have severe and dramatic impacts on native species and their associated ecosystems.

*Ligustrum sinense* presence is correlated to urban areas, but the reason for this correlation is unknown. If *L. sinense* is taking advantage of disturbance created by human development than abiotic conditions should differ by dominant land cover and *L. sinense* should have higher growth or survival in developed watersheds. If *L. sinense* is competitively dominant then it should have higher survival and growth than native species in all watersheds. To test these questions I conducted a transplant seedling experiment where I monitored the growth and survival of *L. sinense* against three native species for two growing seasons in nine watersheds with different land covers. By monitoring both abiotic conditions along with the biotic responses of the transplant seedlings I can infer what is the mechanism driving *L. sinense* invasion. The abiotic conditions where similar between watersheds and do not support a disturbance gradient. Likewise growth and survival of *L. sinense* was not related to watershed development. These results indicate that *L. sinense* is not driven by disturbance and that no floodplain forests are resistant to invasion. In comparison to the native species, *L. sinense* had the highest mean survival. *Ligustrum sinense* also had significantly less herbivory than native species. These results indicate that *L. sinense* is a strong invader that does not need disturbance events to invade habitats. Further surveys revealed that sites that had been invaded earliest had the highest amounts of *L. sinense*. This shows that past propagule pressure is an extremely important element for explaining current distributions. Management of both invaded areas and prevention of new propagule introductions are needed to avert further spread of *L. sinense*.

## BIOGRAPHICAL SKETCH

Like most children, Brian Taylor Greene was born. Brian had the good fortune of being born, but not raised in South Carolina. Growing up on the shores of the Chesapeake Bay, Brian enjoyed a childhood of exploring creeks, hiking through the forest, and catching all sorts of biodiversity. Inspired by his love for the outdoors, a spirit of adventure, and an intense curiosity about nature, Brian excelled in science and chose to pursue additional education about the world around him. This led him back to South Carolina, where he studied Biology at Wofford College. The addiction to science only intensified with various experiences centered on catching reptiles and amphibians all over the western hemisphere. But with further education a deep respect and awe for plants was born in him that unknowingly lead him to an honors project studying invasive privet. The immensity of the problem challenged Brian and left many questions nagging after graduation.

After teaching and traveling couldn't drown out those questions Brian decided to apply to graduate school. Despite being called a "bad statistic", Brian was able to find a back door into Cornell. Study at the Department of Natural Resources allowed for both applied and theoretical training in ecological sciences, but more importantly the stimulus of an intellectual climate. But his greatest joy was always fieldwork, so for a third time Brian returned to South Carolina looking to answer questions about privet and man. So in summers he sweated in the floodplain forests and in winters he froze at Cornell. And even though all his hypotheses were wrong, the questions were right. Through much joy and some pain, Brian finally had the answers to his questions and could move on.

This thesis is dedicated to Louisa and Oakley Coburn

for all their support, love and laughter.

Thank you.

# ACKNOWLEDGEMENTS

Since graduate school doesn't happen without a lot of money, I want to start by thanking the organizations that made it possible. A Graduate Research Fellowship from the National Science Foundation was an incredible source of support. Funding for research was provided by the Graduate School of Cornell, the South Atlantic chapter of the Society of Wetland Scientists, the Biogeochemistry and Environmental Biocomplexity IGERT, and additional funding provided by Dr. Bernd Blossey.

I would like to thank my committee, Drs. Mark Bain, Barbara Bedford and M. Todd Walter for providing insights, criticisms, advice, and energy into my work; my project and myself greatly benefited. A special thanks goes to Dr. Bernd Blossey, my major advisor, for his support, effort, enthusiasm, encouragement and understanding.

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I want to give a big thanks to all my friends for their support, but especially to Ann Armstrong, Kirk Parks and Mary Yates. Even though they don't really understand what I do and are often far away, my family provided immense support and encouragement that I could always feel. Louisa and Oakley Coburn were a huge part of this and I wouldn't have wanted to do it without them.

Personally I want to thank Apple, Brickhouse Campground, Charlie Mops, God, Midway Barbeque, The Nu-way, WNCW, and Zarathustra. And not necessarily in that order.

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Lost in the Weeds: *Ligustrum sinense* reduces native plant growth and survival.

**Summary**

1. Invasive plant species are reported to negatively affect native plant species, but recent research questioned methodology and interpretation of experiments that invasive plants are the primary cause of native plant species declines.

2. I used a combination of field observations and a transplant experiment to investigate the influence of an invasive shrub, *Ligustrum sinense* (Chinese Privet) on native plant species in floodplain forests of the Piedmont ecoregion of South Carolina, USA. I selected 12 floodplain forests where I conducted vegetation surveys documenting abundance and cover of all herbaceous and woody plant species. In addition, I selected a single site to establish experimental transplant gardens where I compared survival and growth of *L. sinense* and four native species transplanted into a mature *L. sinense* stand and an uninvaded adjacent area.

3. The vegetation survey demonstrated a strong negative relationship between *L. sinense* and herbaceous vegetation. As *L. sinense* cover increased, herbaceous cover, herbaceous height, total plant abundance, and native species richness significantly decreased.

4. The transplant experiment showed drastic effects of *L. sinense* on native plant seedlings. Only 5% of native plants survived two growing seasons under the mature *L. sinense* stand and native seedling growth was substantially reduced. Conversely, *L. sinense* seedlings had higher survival and grew taller under *L. sinense* compared to the uninvaded area.

5. Synthesis: The results from both the vegetation survey and transplant experiment show that *L. sinense* is directly reducing growth and survival of native plant species.

By taking an approach that combines multiple field sites and local level investigations this research demonstrates that *L. sinense* is that causal agent of plant declines in floodplain forests. Invasion of *L. sinense* removes the herbaceous understory and prevents the regeneration of canopy trees by suppressing seedlings. This research supports the hypothesis that certain invasive plants can have severe and dramatic impacts on native species and their associated ecosystems.

**Introduction**

Invasive species are a pervasive part of the landscape. Humans have transported species across the planet for thousands of years, but only in the past few decades has our attention focused on species that cause ecological and economic harm (Elton 1958; Wilcove et al. 1998; Mack et al. 2000). However, recent studies question the general assumption that all introduced species cause ecological or economic problems (Gurevitch & Padilla 2004; MacDougall & Turkington 2005; Ricciardi & Cohen 2007).

Uncertainty about ecosystem impacts of invasive species resides, in part, in common methodologies to assess such impacts by comparing invaded and uninvaded areas (Martin 1999; Burton, Samuelson, & Pan 2005), or comparing plant diversity and richness before and after removal of invasive species (Merriam & Feil 2002). Unfortunately such studies are unable to separate direct negative effects of the invasive species from abiotic or biotic habitat conditions causing declines of native species or favoring introduced taxa (Gorchov & Trisel 2003; Nuzzo, Maerz, & Blossey 2009). Fortunately, experiments explicitly testing for effects of invasive on native species are increasing (Gorchov & Trisel 2003; Hartman & McCarthy 2004; Morrison & Mauck 2007; Siemens & Blossey 2007; Galbraith-Kent & Handel 2008; Osland, Pahl, & Richardson 2009). A second approach is to directly investigate

potential mechanisms that promote invasive species' dominance, such as allelopathy, light reduction or competition (i.e, Siemens & Blossey 2007) or their impact on secondary consumers (Maerz, Blossey, & Nuzzo 2005; Brown et al. 2006). Results from these more nuanced experiments can provide strong direct evidence that invasive species, and not other associated factors, are the cause of native plant declines. Moreover, understanding mechanisms of how introduced species impact native species or communities will allow development of mitigation or management techniques that target the root cause and not simply a symptom of other underlying stressors (Nuzzo, Maerz, & Blossey 2009).

*Ligustrum sinense* Loureiro (Chinese Privet), a horticultural introduction to the United States in the 1850s (Coates 1965), is a shrub with vigorous growth and can obtain 9 m in height. Native to China, *L. sinense* is a member of the Oleaceae, a family with no native representatives of the genus *Ligustrum* in North America (Weakly 2008). In the southeastern United States *Ligustrum* is a common non-native genus in riparian habitats (Merriam 2003) and has invaded an estimated 1.09 million forested hectares (Miller, Chambliss, & Oswalt 2008). Currently *L. sinense* ranges from Massachusetts south to Florida and west to Texas and is considered an invasive species in many states, including South Carolina where it is listed as a severe threat (SC-EPPC 2008). *Ligustrum sinense* retains most of its leaves throughout the year and a mature individual can produce abundant fruit (Morris, Walck, & Hidayati 2002). Birds eat and disperse this fruit (Strong, Brown, & Stouffer 2005) and the fruit can float in water for up to two weeks (Greene, Personal Observations). *Ligustrum sinense* is tolerant of both flooding and low light levels making it well suited to invade floodplain forests (Brown & Pezeshki 2000). Areas invaded by *L. sinense* are reported to have lower native species richness, abundance and cover (Loewenstein & Loewenstein 2005; Wilcox & Beck 2007; Burton & Samuelson 2008) and *L. sinense*

removal increases native species richness (Merriam & Feil 2002; Vidra, Shear, & Stucky 2007) and height and cover of native *Arundinaria gigantea* (Walter) Muhlenberg (Giant Cane) (Osland, Pahl, & Richardson 2009).

In this study I examined the influence of *L. sinense* presence on plant individuals and communities using both observational and experimental designs. In the observational study I examined vegetative characteristics of multiple field sites to ascertain any landscape-level correlation between *L. sinense* and other plant species. Based on previous research and observations, I hypothesized that increased cover of *L. sinense* would be negatively correlated with herbaceous cover, abundance, height and native species richness. I used a transplant experiment (with seedlings planted into and outside of a *L. sinense* canopy) to test if *L. sinense* was a direct cause of the reduction in plant performance. I hypothesized that native plant seedlings would have lower growth and survival under mature stands of *L. sinense* than native plant seedlings grown in the absence of *L. sinense*.

**Methods**

STUDY SITES

This study examined 12 different floodplain forests across the Piedmont ecoregion of South Carolina (Figure 1-1). Characterized by rolling hills and alluvial streams that are flanked by floodplain forests, the Piedmont is located between the fall line and the Blue Ridge Escarpment (Porcher & Rayner 2001). I selected sites as part of a larger study to identify land use influences on invasive species distribution (B.T. Greene, Chapter 2). I visited all potential sites in late May 2007 to ascertain viability for the study. I rejected sites that had active signs of livestock grazing, had been recently logged, or had a floodplain width less than 100 m. In total 12 hydrologically independent floodplain forests and their associated watersheds were chosen for the

study. The National Wetland Inventory (USFWS 2009) identified all sites as palustrine forested wetlands that are temporarily flooded. Floodplain forests are distinguished by periodic flooding of the adjacent streams (Hook et al. 1994) that can leave the area inundated with standing water for up to five days (B.T.Greene, Personal Observations). Sites are secondary hardwood forests with a dominant canopy of *Acer negundo* L., *Fraxinus pennsylvanica* Vahl, *Celtis laevigata* Willd., *Platanus occidentalis* L., and *Populus deltoides* Marsh. Native shrub species *Ilex decidua* Walter, *Asimina triloba* (L) Dunal, *Carpinus caroliniana* Walter, and *Arundinaria tecta* (Walter) Muhlenburg are common, but sparsely distributed. The understory is dominated by an herbaceous community primarily of grasses and sedges. All sites had signs of deer presence (browse, trails, and rubbings) and contained non-native earthworms. The region has a warm-humid temperate climate type with a mean annual temperature of 15.8°C and mean annual precipitation of 116 cm, but the region experienced a drought for the entire time of this study as indicated by the Palmer Hydrologic Drought Index (NCDC 2009).

## VEGETATION SURVEY

I surveyed all 12 field sites for vascular plants during the peak of the growing season from 11 June to 15 July 2007. At each site, except Lawson's Fork and Reedy River (sites 1 and 2 respectively, Figure 1-1), I selected a 200 m stream reach at least 75 m from the nearest forest edge. At Lawson's Fork and Reedy River I used a 100 m stream reach to ensure contiguous habitat. At all sites I randomly located five transects along this reach. Each transect ran along a compass heading perpendicular to the stream and extended 100 m into the floodplain interior. Along each transect, I randomly located six plots to measure plant composition (N= 30 plots/site). I nested a $1m^2$ square (herbaceous plot) inside a 2x5m area (shrub plot) where I identified,

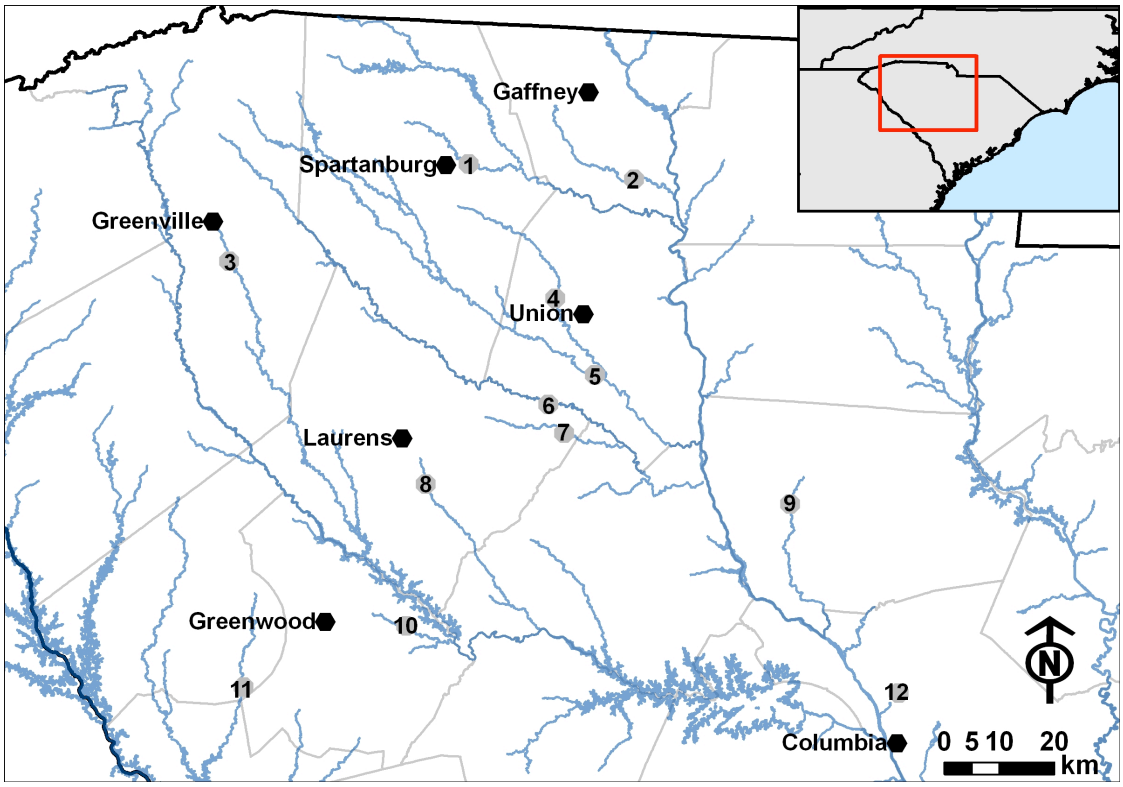

Figure 1-1 Field site locations and their associated streams, major cities (black hexagons) and counties (grey outlines) in the Piedmont ecoregion of South Carolina. Sites: Lawson's Fork Creek (1), Thicketty Creek (2), Reedy River (3), Fairforest Creek (4), Tyger River (5), Enoree River (6), Duncan Creek (7), Little River—Laurens County (8), Little River – Fairforest County (9), Wilson's Creek (10), Long Cane Creek (11), Crane Creek (12).

counted all stems and visually estimated herbaceous cover (%) for each species. In addition, I recorded height of the tallest plant in each corner and then created a mean maximum herbaceous height. Not all plants had identifiable characteristics during the survey period requiring some species to be grouped by genus using identical groupings at all sites. I used the $10m^2$ shrub plot to identify, count all individuals, and visually estimate cover (%) for each shrub species. The shrub level included both woody and herbaceous plants that were taller than the mean maximum herbaceous height, but did not reach above 8 m total height.

TRANSPLANT EXPERIMENT

I used *Acer negundo* L. var. *negundo*, a common native floodplain tree, *Boehmeria cyclindrica* (L.) Swartz a common wetland forb, *Carex tribuloides* Wahlenburg var. *tribuloides* a floodplain forest sedge and *Chasmanthium latifolium* (Michaux) Yates, a common understory grass of floodplain forests as representative native species for my transplant experiment. I incorporated *L. sinense* into my experiment to compare the response of native species and the invader to the same growing conditions.

I collected seeds for all species in winter 2007-2008. I stored *C. latifolium* and *L. sinense* seeds dry at 22 ˚C in paper bags and *A. negundo*, *B. cyclindrica*, and *C. tribuloides* seeds in the dark at 5 ˚C in plastic bags with moist paper towels. In mid-March 2008 I scattered seeds on a moist 50:50 mixture of Pro-Mix potting soil (Farfard Canadian growing mix No. 1-P, Agawam, Massachusetts, USA) and playground sand in plastic trays in a greenhouse maintained at 25 ˚C with a 12 hr photoperiod. I watered trays periodically from above to maintain surface moisture for the developing seedlings. After nine weeks I selected 40 individuals of similar size from each species (Mean height (cm) ± SE; *A. negundo* 12.0 ± 0.4; *B. cyclindrica* 4.3 ± 0.2; C. *tribuloides* 11.4 ± 0.7; *C. latifolium* 9.1 ± 0.2; *L. sinense* 4.6 ± 0.1) . For all species except for *A. negundo* sufficient seeds germinated to provide seedlings for the experiment. As a replacement, I collected 4-leaved *A. negundo* seedlings on 26 April 2008 at Lawson's Fork Creek.

I established two experimental grids in a floodplain forest at Lawson's Fork Creek; the first in a 30 by 50 m homogenous stand of mature *L. sinense* at least 2 m from the edge (LS present), the second 15 m away from the edge of the *L. sinense* stand but under the same native tree canopy (LS absent). The first grid had 95% cover of *L. sinense* with mainly bare ground and leaf litter underneath, while the second showed a herbaceous community dominated by sedges and grasses including the invasive

*Microstegium vimineum* (Trin.) A. Camus. Each grid consisted of 100 1 x 1 m cells with two adjoining rows of 10 cells separated by a 1m wide walkway from the next two adjoining rows for a total of 10 rows. I divided individuals of each transplant species randomly into two groups of 20. I selected an individual at random from this group and planted it bare root into the center of a cell directly into the extant vegetation. To alleviate immediate plant competition and allow for establishment of transplants, I anchored a 20 x 20 cm black plastic sheet (6mm) to the substrate using metal nails. Each plastic sheet contained a $25cm^2$ center hole where the seedling was planted. I marked all seedlings individually with a numbered metal ID tag to ensure proper identification on subsequent visits. Plastic sheets were quickly overgrown by vegetation but made relocation much easier.

I planted 20 individuals of each species into each grid (total = 200 individuals) on 12 and 13 May 2008. I replaced dead individuals that most likely died due to transplant shock only on the first subsequent visit after one week but did not replace dead or dying individuals in subsequent weeks. I watered plants twice, once upon planting and again at the first re-visit. During the first growing season I monitored sites every other week in May, June and July, once in mid-August, and once in late October (9 sample periods over 24 weeks). In the second growing season I visited all sites in February, May, and July (3 sample periods over 39 weeks) to measure plant growth and record survival and herbivory. I counted individuals as alive if green photosynthetic tissue was present. I measured height (to 0.5 cm accuracy) to the apical meristem for *A. negundo, B. cyclindrica,* and *L. sinense* and to the height leaves reached when held erect for *C. tribuloides* and *C. latifolium*. I also recorded the number of leaves for *A. negundo* and *C. latifolium* and stem or leaf herbivory for all species (presence/absence).

STATISTICAL ANALYSIS

I used linear regression to assess relationships of herbaceous cover, mean maximum herbaceous height, total number of herbaceous stems, and herbaceous native species richness/$m^2$ with mean *L. sinense* cover at each site. I used a nonparametric Mann - Whitney test to compare initial and final heights of individuals, maximum growth from both seasons, and herbivory (%) in either treatment group (LS present or absent) for each species. I calculated maximum growth as the greatest height increase from the initial height of surviving individuals for each growing season. I used nonparametric Mann - Whitney because seedling mortality resulted in uneven numbers among groups and non-normal distribution. I used Generalized Estimating Equations (GEE) (Liang & Zeger 1986) to compare change in the number of leaves for *A. negundo* and *C. latifolium* with treatment as a fixed effect using a Poisson distribution. I created survival curves for each species and used Binomial regression with survival as a function of treatment and initial height using a generalized linear model. I used R (R Development Core Team 2008) for all analyses.

**Results**

VEGETATION SURVEY

I found significant negative correlations for herbaceous cover ($R^2 = 0.354$, P =0.04), total herbaceous count ($R^2 = 0.356$, P =0.04), and herbaceous native species richness/$m^2$ ($R^2 = 0.499$, P =0.01) as a function of mean *L. sinense* cover (Figures 1-2 – 1-4). Mean maximum herbaceous height (Figure 1-5) also declined as mean *L. sinense* cover increased, but this relationship was only marginally significant ($R^2 = 0.318$, P =0.056).

TRANSPLANT EXPERIMENT

At the end of 63 weeks survival rates (%) for all native species, except *B. cyclindrica,* were higher in the LS absent grid than under *L. sinense* (Figures 1-6 – 1-10). While *B. cylindrica* survival was higher outside *L. sinense* in the first growing season (Figure1 - 7), no individuals from either group survived the winter. Of 20 individuals planted under *L. sinense* for each *A. negundo*, *C. latifolium*, and *C. tribuloides* only one individual of each species survived the entire 63-week experiment. However, *L. sinense* seedlings had higher survival under *L. sinense* than outside (Figure 1-10). Treatment was a statistically significant predictor of survival (Table 1-1) for all species, except for *B. cylindrica* and *L. sinense*. Seedling heights at planting did differ between treatment groups for *B. cylindrica* (W = 305.5, P = 0.004) and *C. latifolium* (W = 105.5, P = 0.01) with slightly taller plants in the LS absent treatment but, initial height at planting was not significantly related to survival for any species (Table 1-1).

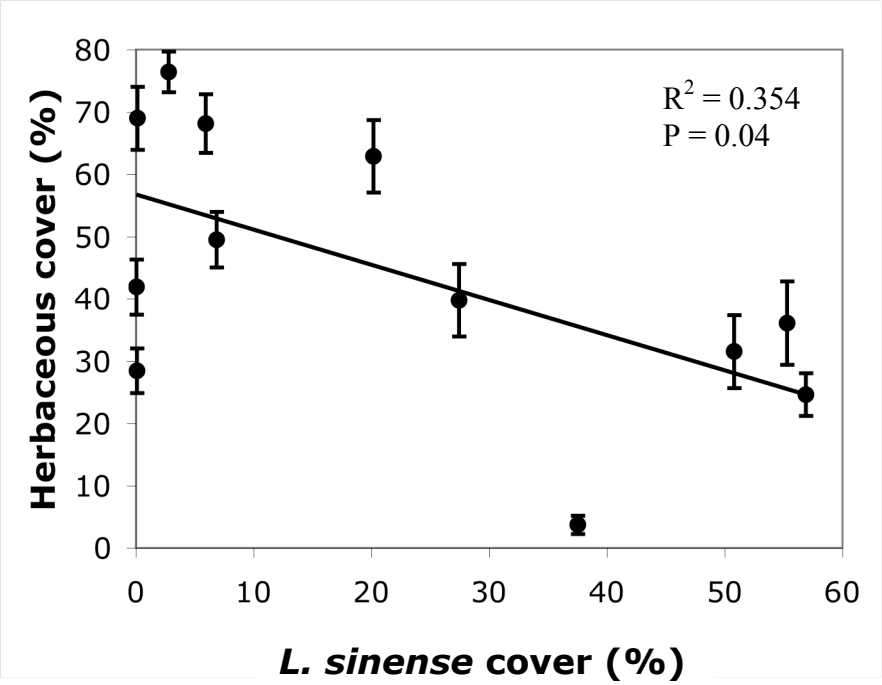


Figure 1-2 Herbaceous cover (%) as a function of mean *L. sinense* cover (%). Data are means ± 1SE of 30 plots at each of 12 floodplain forests.

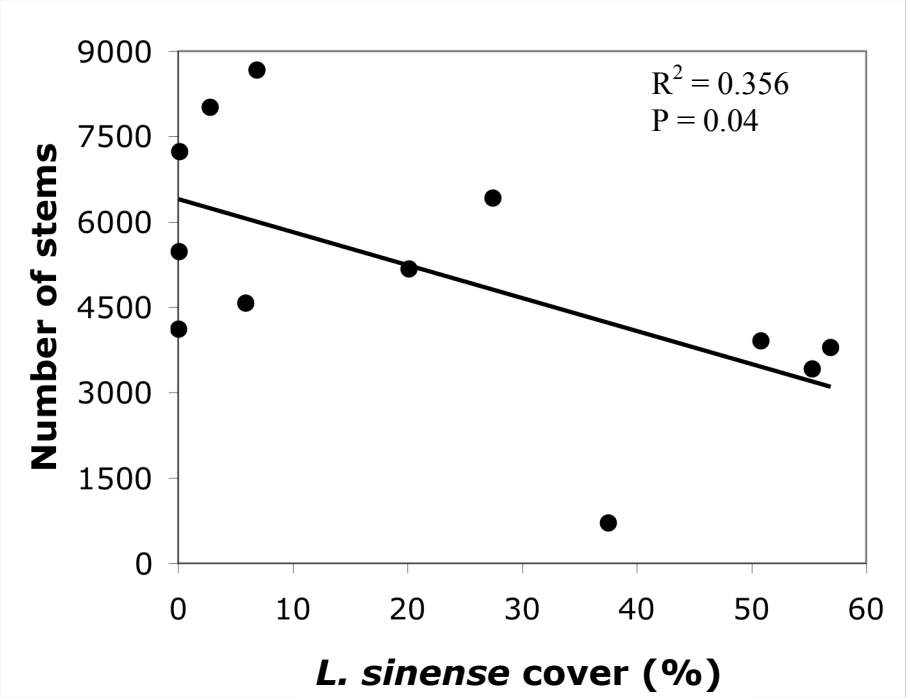


Figure 1-3 Total number of herbaceous stems per site as a function of mean *L. sinense* cover (%). Data represent the sum of 30 plots at each of 12 floodplain forests.

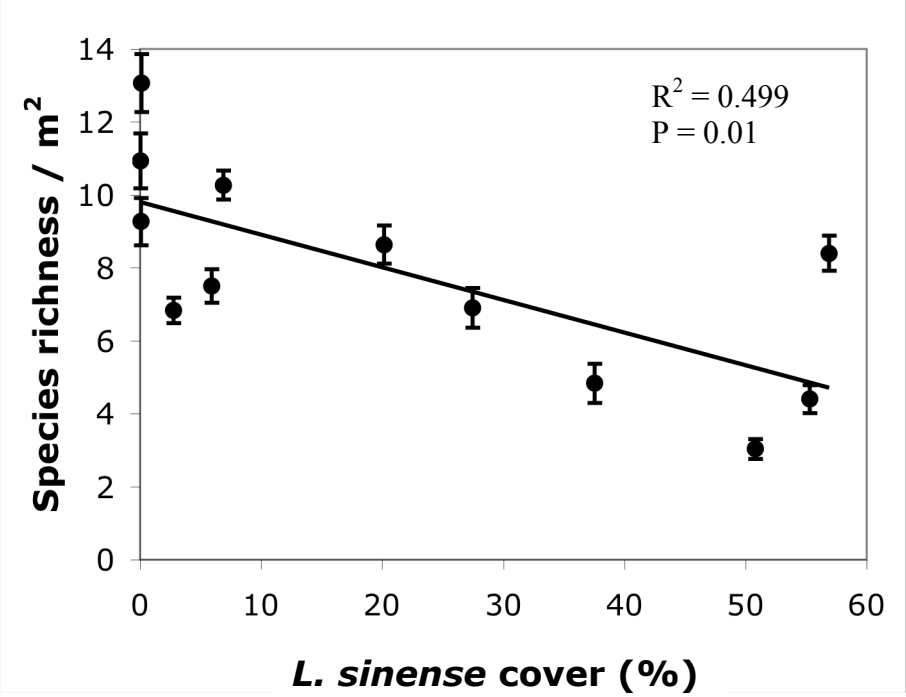


Figure 1-4 Herbaceous native species richness per $m^2$ as a function of mean *L. sinense* cover (%). Data are means ± 1SE of 30 plots at each of 12 floodplain forests.

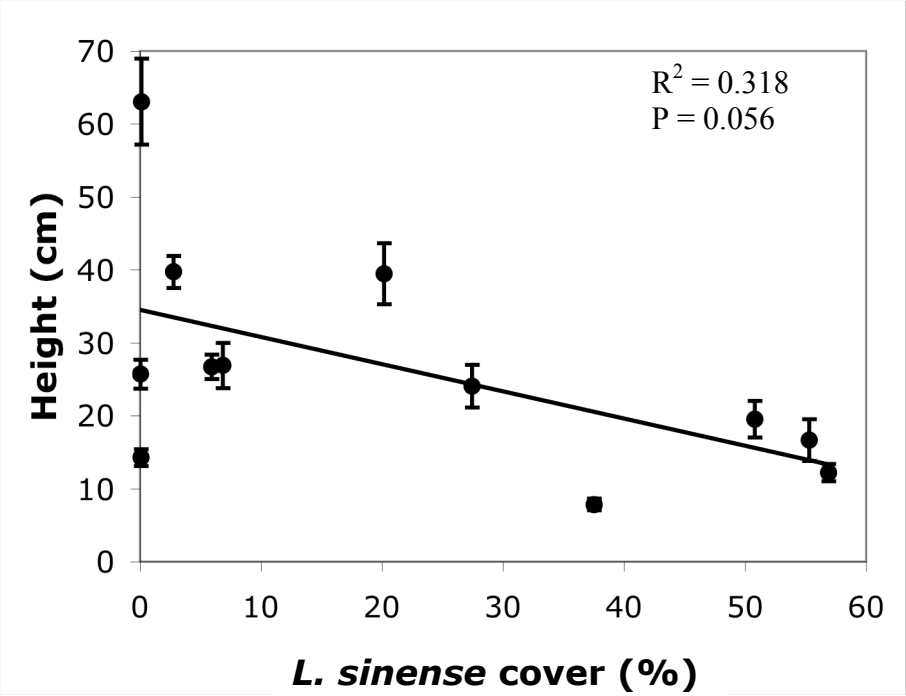


Figure 1-5 Herbaceous maximum height (cm) as a function of mean *L. sinense* cover (%). Data are means ± 1SE of 30 plot means at each of 12 floodplain forests.

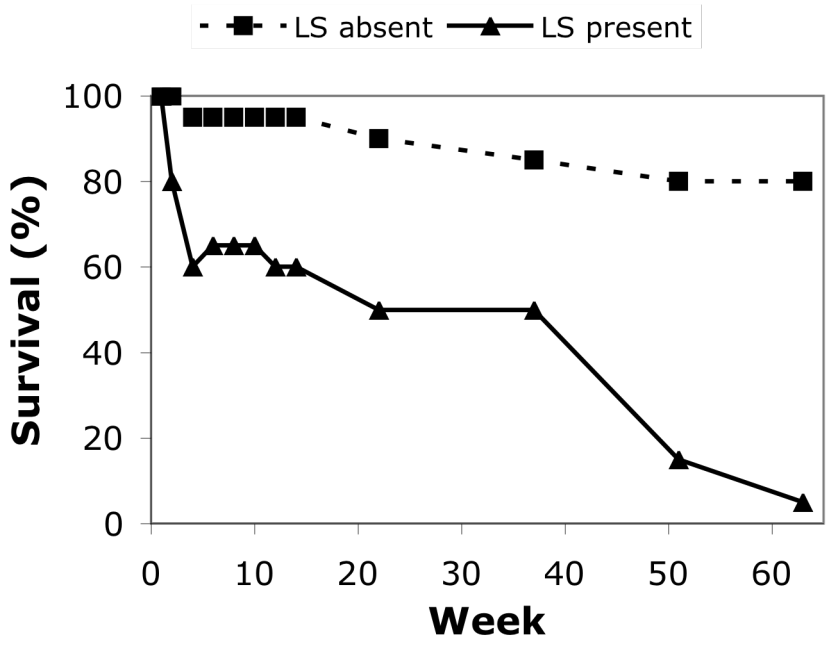


Figure 1-6 Survival (%) of *Acer negundo* seedlings planted under *L. sinense* canopy (LS present) or into adjacent uninvaded floodplain forest (LS absent). N = 20 individuals/treatment.

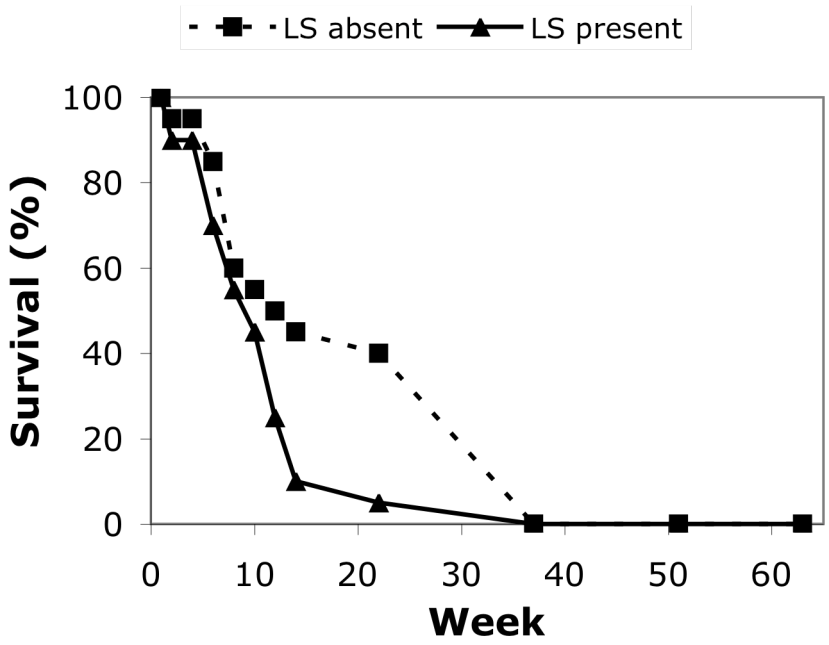


Figure 1-7 Survival (%) of *Boehmeria cyclindrica* seedlings planted under *L. sinense* canopy (LS present) or into adjacent uninvaded floodplain forest (LS absent). N = 20 individuals/treatment.

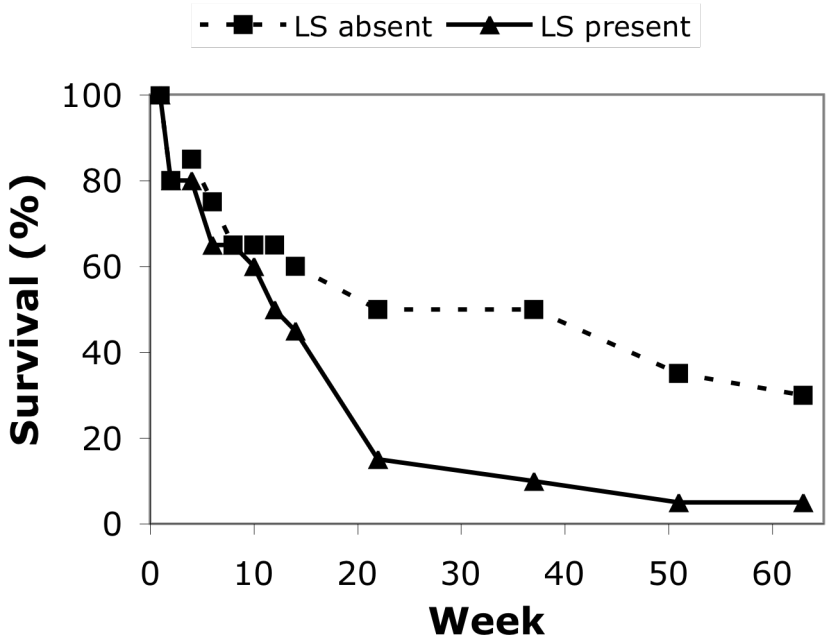


Figure 1-8 Survival (%) of *Carex tribuloides* seedlings planted under *L. sinense* canopy (LS present) or into adjacent uninvaded floodplain forest (LS absent). N = 20 individuals/treatment

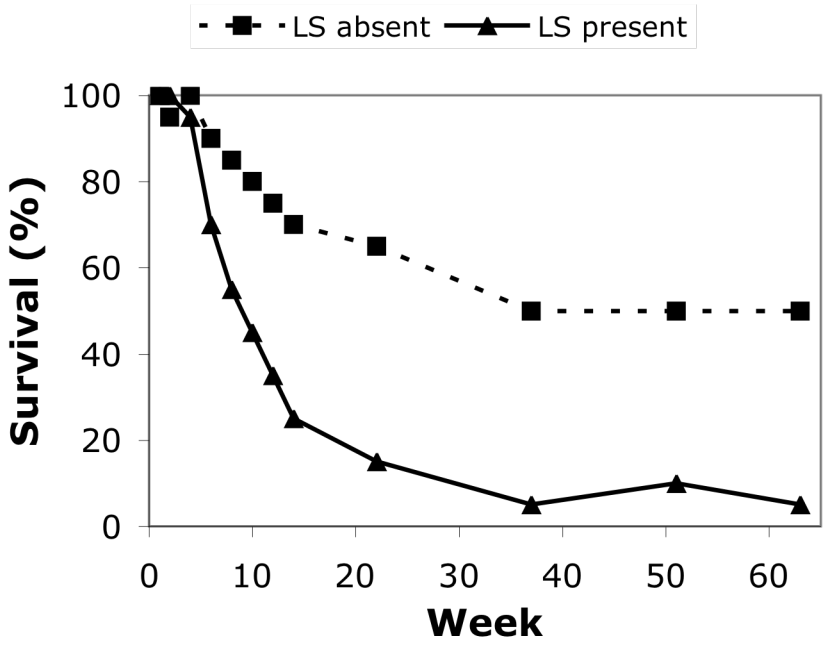


Figure 1-9 Survival (%) of *Chasmanthium latifolium* seedlings planted under *L. sinense* canopy (LS present) or into adjacent uninvaded floodplain forest (LS absent). N = 20 individuals/treatment

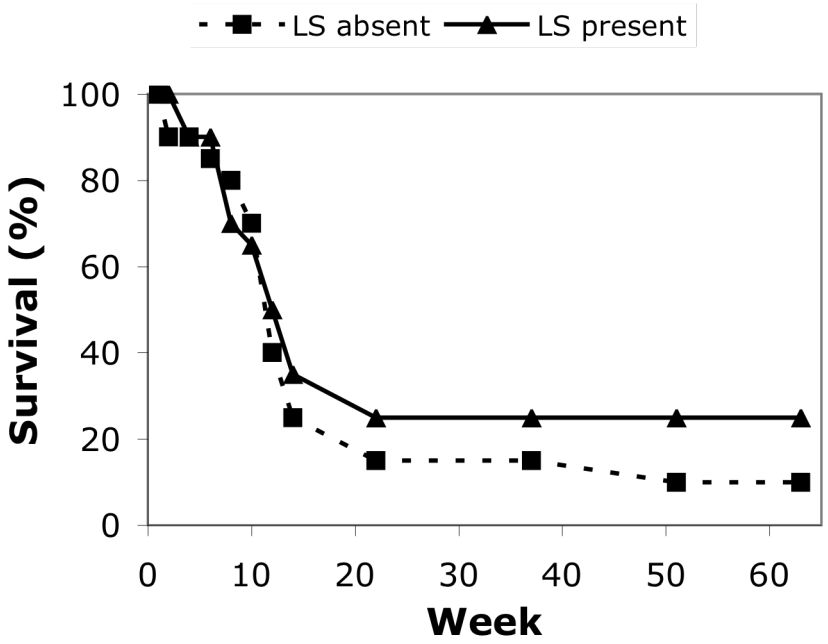


Figure 1-10 -- Survival (%) of *Ligustrum sinense* seedlings planted under *L. sinense* canopy (LS present) or into adjacent uninvaded floodplain forest (LS absent). N = 20 individuals/treatment

Table 1-1 Results of a binomial GLM testing survival as a prediction of treatment group and initial heights. Significant results are in bold. AN = *Acer negundo*, BC = *Boehmeria cyclindrica*, CL = *Chasmanthium latifolium*, CT = *Carex tribuloides*, LS = *Ligustrum sinense*

| | Estimate | SE | *z*-value | Pr > \|z\| |
|---|---|---|---|---|
| Treatment | | | | |
| AN | -4.63 | 1.32 | -3.52 | **$4.29 \times 10^{-4}$** |
| BC | $1.27 \times 10^{-14}$ | $1.27 \times 10^{5}$ | $1.00 \times 10^{-19}$ | 1.000 |
| CL | -2.59 | 1.15 | -2.26 | **0.024** |
| CT | -2.50 | 1.27 | -1.96 | **0.049** |
| LS | 1.13 | 0.92 | 1.24 | 0.216 |
| Initial Height | | | | |
| AN | 0.50 | 0.27 | 1.88 | 0.060 |
| BC | $3.21 \times 10^{-15}$ | $5.23 \times 10^{4}$ | $6.13 \times 10^{-20}$ | 1.000 |
| CL | 0.40 | 0.34 | 1.18 | 0.240 |
| CT | -0.36 | 0.22 | -1.67 | 0.094 |
| LS | -0.10 | 0.44 | -0.24 | 0.811 |

In the first growing season all species had higher growth outside *L. sinense* (Figure 1-11) and differences are significant *B. cylindrica* (W = 366, P < 0.0001); *C. tribuloides* (W = 315.5, P = 0.001); *C. latifolium* (W = 305, P = 0.004); *L. sinense* (W = 303, P = 0.004); except for *A. negundo* (W = 233.5, P = 0.32). In the second growing season only *A. negundo* (W = 167.5, P < 0.0001) growth was significantly different between groups with higher growth outside *L. sinense* (Figure 1-12). *Chasmanthium latifolium* (W = 20, P = 0.09) and *C. tribuloides* (W = 15, P = 0.33) had higher mean growth in the second season, but probably due to low seedling survival under the *L. sinense* canopy, differences in growth were not statistically significant. In the second growing season *L. sinense* seedlings grew taller under *L. sinense* canopy, but differences in growth were not significant (W = 4, P = 0.37). When viewed as percent increase in mean maximum growth, native species were orders of magnitude higher in the LS absent compared to LS present.

The numbers of leaves on individuals were consistently higher in the LS absent treatment and this was marginally significant for *A. negundo* (Figure 1-13) and significant for *C. latifolium* (Figure 1-14). For *A. negundo*, seedlings in both treatment groups started with four leaves and during the first growing season stress and herbivory resulted in a general decline, plants in the second season recovered, at least in the LS absent treatment (Figure 1-13). *Chasmanthium latifolium* individuals started with four leaves and showed a gradual increase in the first growing season in both treatments, but after the winter dormancy only plants in the LS absent treatment greatly increased (Figure 1-14). Presence-absence of herbivory varied greatly among sampling periods (*A. negundo* 0-75%, *B. cylindrica* 0-100%, *C. tribuloides* 0-100%, *C. latifolium* 0-100%, *L. sinense* 0-50%), but there was no significant difference in herbivory between treatments for any species ($P > 0.05$). **

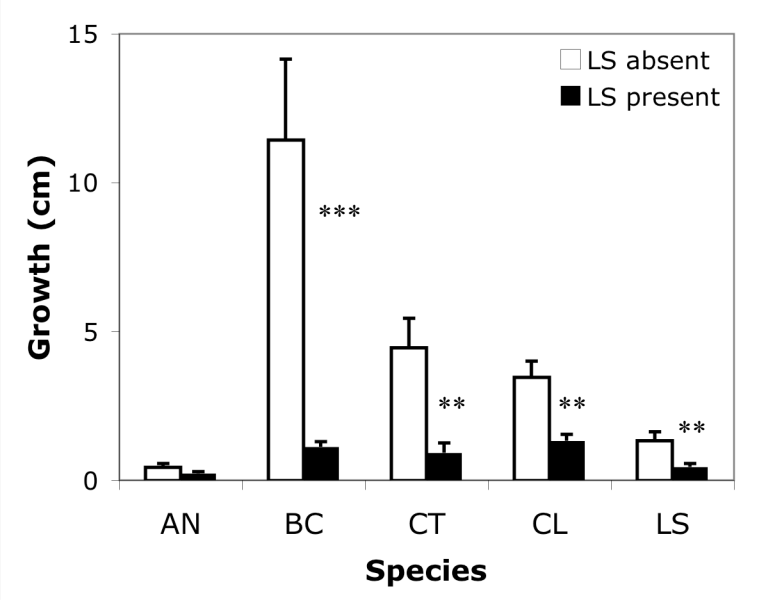


Figure 1-11 First growing season maximum growth (cm) for different seedlings in the presence (LS present) or absence (LS absent) of *L. sinense*. Data are means + 1 SE of N = 20 for each species/treatment. Asterisks indicate significant differences between treatments based on a Mann-Whitney Test (*P < 0.05, **P < 0.01, ***P < 0.001). AN = *Acer negundo*, BC = *Boehmeria cyclindrica*, CL = *Chasmanthium latifolium*, CT = *Carex tribuloides*, LS = *Ligustrum sinense*

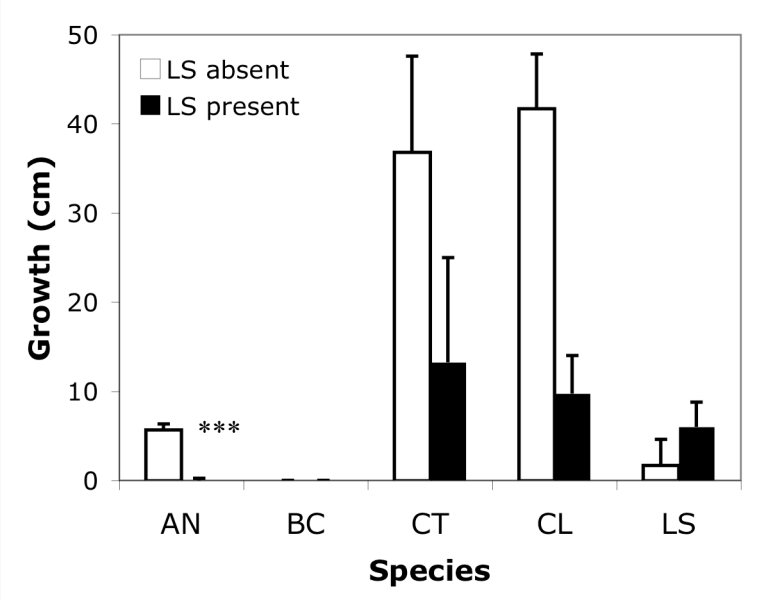


Figure 1-12 Second growing season maximum growth (cm) for different seedlings in the presence (LS present) or absence (LS absent) of *L. sinense.* Data are means + 1 SE of LS absent N: AN= 17, BC=0, CT=10, CL=11, LS=3. LS present N: AN = 10, BC=0, CT=2, CL=2, LS=5. Asterisks indicate significant differences between treatments based on a Mann-Whitney Test (*P < 0.05, **P < 0.01, ***P < 0.001). Same species codes as Figure 1-11.

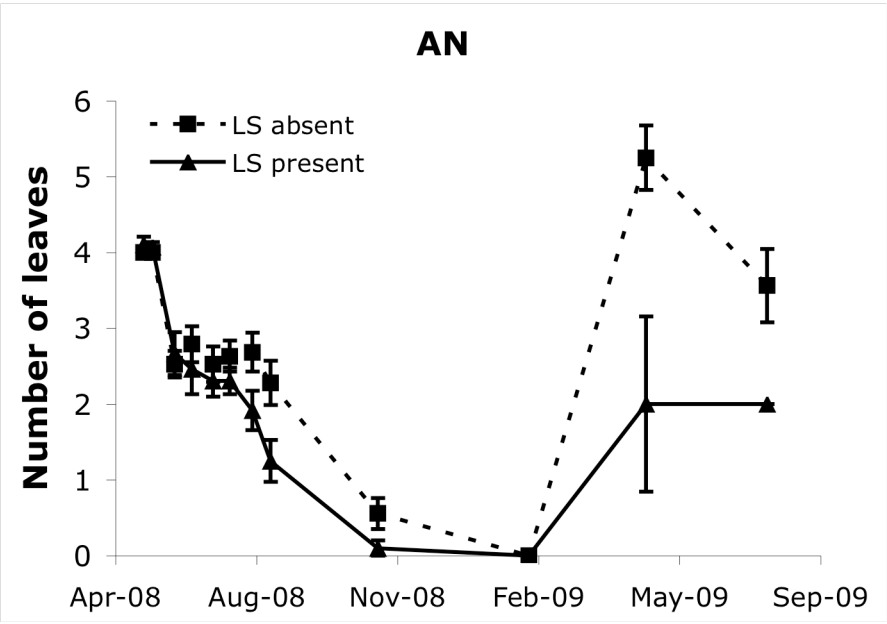


Figure 1-13 Number of *Acer negundo* leaves/plant for transplant seedlings growing in the presence (LS present) or absence (LS absent) of *L. sinense* over the 63-week observation period. Data are means (±1SE) of all live individuals in each treatment (up to N =20). Results of the GEE examining the difference in number of leaves as a prediction of treatment group: Estimate = -0.144, SE = 0.075, Wald = 3.68, P = 0.055

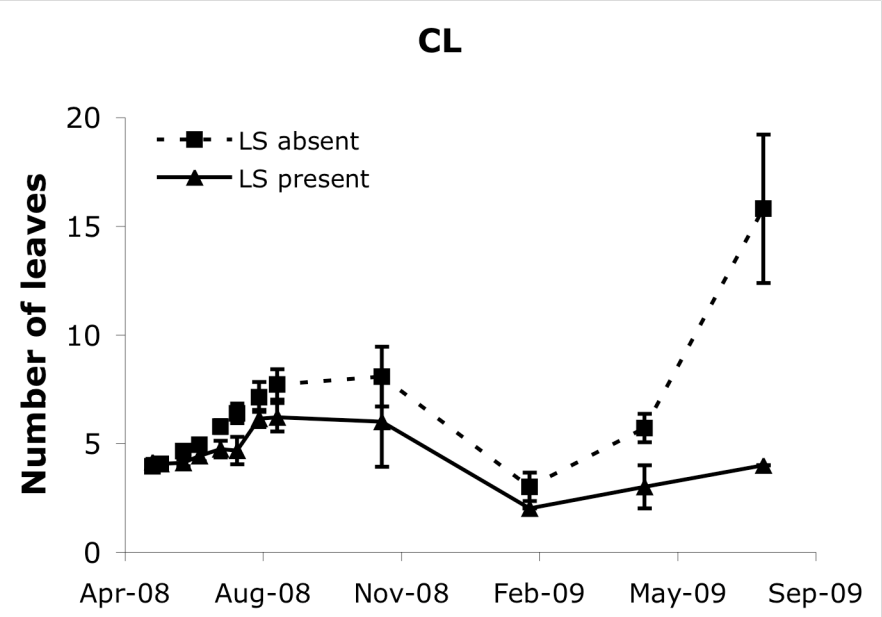


Figure 1-14 Number of *Chasmanthium latifolium* leaves/plant for transplant seedlings growing in the presence (LS present) or absence (LS absent) of *L. sinense* over the 63-week observation period. Data are means of all live individuals per sampling (±1SE) in each treatment (up to N =20). Results of the GEE examining the difference in number of leaves as a prediction of treatment group: Estimate = -0.278, SE = 0.085, Wald = 10.6, P = 0.0011

**Discussion**

Results of my research confirm assumptions that *L. sinense* invasion is negatively affecting native plant species in Piedmont floodplain forests. In vegetation survey plots with high *L. sinense* cover, I observed only sparse herbaceous growth and most of the species were non-native. This closely mirrors the results of my transplant experiment where the invasive *L. sinense* had the highest survival and where few individuals of native species survived and those that survived performed poorly. The results of my vegetation survey demonstrated impoverishment of the local flora in the presence of *L. sinense*, with effects increasing as *L. sinense* cover increases. My transplant experiment confirmed this pattern as cause and effect. Moreover the results indicate a snowballing effect where *L. sinense* continues to reduce survival and growth

of native transplant seedlings ultimately leading to an ever increasing survival and performance difference between seedlings in different treatments in the second growing season. For example, only a single individual of *A. negundo*, *C. latifolium*, and *C. tribuloides* survived the entire 63 weeks under *L. sinense* and growth was greatly suppressed indicating that *L. sinense* exerts a strong selective force on native seedlings. It is noteworthy that the higher growth in the LS absent environment is realized in the presence of *M. vimineum*, itself an invasive species that can reduce diversity and density of plants (Oswalt, Oswalt, & Clatterbuck 2007). This demonstrates further the substantial potential of *L. sinense* to suppress native seedlings, but not the growth of its own recruits.

This combination of observational and experimental results adds to previous evidence (Merriam & Feil 2002; Loewenstein & Loewenstein 2005; Vidra, Shear, & Stucky 2007; Wilcox & Beck 2007; Burton & Samuelson 2008; Osland, Pahl, & Richardson 2009) for negative effects of *L. sinense* at both the landscape and local level and confirms the hypotheses that *L. sinense* reduces plant growth and survival. With no difference in potentially confounding factors such as exotic earthworms (present at all sites) and herbivory (no difference between treatments) the most parsimonious explanation for native species decline is *L. sinense*. While other studies have shown that invasive plants are not the sole cause for poor native plant performance or declines (MacDougall & Turkington 2005; Nuzzo, Maerz, & Blossey 2009) my results show that *L. sinense* is the main cause of native species declines. My results support results reported by Osland, Pahl & Richardson (2009) that *L. sinense* decreased growth and cover of *A. gigantea*. Together these results show that *L. sinense* affects multiple species across several functional groups (forbs, grasses, sedges, and trees). Other invasive species with shrub like growth, *Fallopia* X *bohemica* Chrtek and Chrtková, *Ligustrum robustum* (Roxb.) Blume, *Lonicera maackii* (Ruprecht)

Maximowicz, and *Rhamnus frangula* L., reduce native plant survival (Lavergne, Rameau, & Figier 1999; Gould & Gorchov 2000; Gorchov & Trisel 2003; Fagan & Peart 2004; Siemens & Blossey 2007). Reduction of native species growth is not limited only to invasive shrub species; Beckage et al. (2000) documented reduced seedling abundance under dense stands of the native shrub *Rhododendrom maximum* L. This points out that as a functional group, shrubs can have strong influences on understory growth. Shrub species that form dense sub-canopies diminish the amount of light that reaches the forest floor often leading to reductions in germination or plant growth (Beckage et al. 2000; Siemens & Blossey 2007). Light limitation under dense stands of *L. sinense* appears to be the most probable cause of the reduced growth and survival seen in the transplant experiment, yet further research is needed to evaluate other possible mechanisms. Allelopathy is another possible mechanism for reducing plant growth (Callaway & Aschehoug 2000) and the result that *L. sinense* seedlings had higher growth and survival under same species stands could support a positive feedback hypothesis that mature *L. sinense* creates conditions that favor self-propagation. *Ligustrum sinense* has also been shown to alter arbuscular mycorrhizal fungi occurrence (Greipsson & DiTommaso 2006) and that could be another belowground alteration that disfavors native species growth. While the results of my study cannot identify the specific mechanism by which *L. sinense* reduces native plant growth and survival, it identifies *L. sinense* as the causal agent.

*Ligustrum sinense* is distinct in several ways that make it an extremely successful invasive species. As a shrub species invading a system with few native shrub species, *L. sinense* is functionally distinct. Functional diversity can have a greater effect than species diversity on some ecosystem processes (Tilman et al. 1997). Studies have shown that specific functional groups (Tilman 1997) and higher diversity of functional groups (Dukes 2001; Pokorny et al. 2005) can reduce plant invasions. A non-native

species whose functional group is not present in the existing community is more likely to increase in biomass than a species from a present functional group (Dukes 2001). With few extant shrub species in floodplain forests, *L. sinense* invades these "open niches" and forms dense monocultures that alter the structure from open sub-canopy to dense thickets. As a new genus to North America, *Ligustrum* is taxonomically distinct (Weakley 2008). In the United States Lockwood et al. (2001) examined if taxonomic remoteness was a good predictor for likelihood to invade natural areas and found in two of the three states analyzed that plant species from a family or genus new to a state were more likely to be invasive. While taxonomic remoteness has been criticized for being arbitrary, a more objective approach is phylogenetic relatedness (Proches et al. 2008). A study of Californian grasslands found that species "with high ecological impacts are less closely phylogenetically related to members of the native community than are species that naturalize without having large effects on local native species' diversity or richness"(Strauss, Webb, & Salamin 2006). While no studies have been done on the phylogenetic relatedness of *L. sinense* it can be assumed to be fairly phylogenetically distinct since there are no native congeners and only 24 native species of the Oleaceae family in the continental United States (USDA 2009). *Ligustrum sinense* has severe effects on the floodplain forest community and this is in part due to being both functionally and phylogenetically distinct from the extant community. These effects are likely to amplify in the future with increasing habitat fragmentation and atmospheric $CO_2$, both factors that promote *L. sinense* invasion (Cadenasso & Pickett 2001; Smith et al. 2008; White, Vivian-Smith, & Barnes 2009). The implications of these results have severe direct and indirect consequences. Foremost the direct loss of native species due to *L. sinense* invasion, especially tree species. This is the first study to show that an abundant canopy tree of floodplain forests, *A. negundo*, is inhibited by *L. sinense*. My results show that *L. sinense* is

preventing the regeneration of the forest canopy and other studies have similar conclusions (Merriam & Feil 2002; Loewenstein & Loewenstein 2005; Burton & Samuelson 2008). Even though invaded sites currently have mature canopies, this prevention of recruitment can have long term effects that turn floodplain forests from structurally dominated by mature trees to shrub thickets (Merriam & Feil 2002; Loewenstein & Loewenstein 2005). Canopy trees have a critical role in maintaining abiotic and biotic functions and their loss would fundamentally alter the properties of floodplain forests.

These results provide further evidence that mature forest ecosystems are not resistant to invasion, but are threatened by invasive shade tolerant exotics (Martin, Canham, & Marks 2009). *Ligustrum sinense* is lowering the productivity of floodplain forests by reducing plant growth and survival. The highest rate of *L. sinense*'s aboveground net primary productivity (ANPP) was 69.5% lower than the highest rate of ANPP by a native floodplain forest community (Brantley 2008). This will have effects on long-term carbon sequestration and nutrient retention in these wetlands. Native species can take advantage of new food resources that *L. sinense* provides (Stromayer et al. 1998, Strong, Brown, & Stouffer 2005). This rapid adoption of a new food source might explain why Wilcox & Beck (2007) saw no reduction in songbird richness or density with *L. sinense* invasion. Changes in resource use are not limited to terrestrial systems. Floodplain forests have strong terrestrial-aquatic linkages due to allochthonous inputs. With invasive species replacing native species, changes in allochthonous inputs to streams can affect community composition of consumers (Lecerf et al. 2005) and influence the development of larval amphibians (Cohen 2009). Results of my study show that *L. sinense* is having a landscape level effect across the floodplain forests of the Piedmont. These wetlands are important areas for biodiversity, carbon storage, and resource production, all of which are threatened by *L.*

*sinense* invasion. These forests also have multiple societal values (timber production, recreation, aesthetics) that make them important to conserve. In order to maintain the long-term sustainability of floodplain forests in the southeastern United States, policy makers and land managers need to create strategies and polices (Chornesky et al. 2005) to reduce *L. sinense* abundance. This includes supporting methods to control *L. sinense* (Harrington & Miller 2005; Zhang, Sun, & Hanula 2009) and identifying the mechanisms that promote *L. sinense* invasion so that they can be prevented.

REFERENCES

Beckage, B., Clark, J.S., Clinton, B.D. & Haines, B.L. (2000) A long-term study of tree seedling recruitment in southern Appalachian forests: the effects of canopy gaps and shrub understories. *Canadian Journal of Forest Research*, **30**, 1617 – 1631.

Brantley, E.F. (2008) *Influence of Chinese Privet on Riparian forests of the southern piedmont: Net Primary Productivity, carbon sequestration, and native plant regeneration*. PhD Thesis, Auburn University.

Brown, C.E. & Pezeshki, S.R. (2000) Study on waterlogging as a potential tool to control *Ligustrum sinense* populations in Western Tennessee. *Wetlands*, **20**, 429–437.

Brown, C. J., Blossey, B., Maerz, J. C. & Joule, S. J. (2006) Invasive plant and experimental venue affect tadpole performance. *Biological Invasions,* **8,** 327–338.

Burton, M. & Samuelson, L. (2008) Influence of urbanization on riparian forest diversity and structure in the Georgia Piedmont, US. *Plant Ecology*, **195**, 99–115.

Burton, M.L., Samuelson, L.J. & Pan, S. (2005) Riparian woody plant diversity and forest structure along an urban-rural gradient. *Urban Ecosystems*, **8**, 93–106.

Cadenasso, M.L. & Pickett, S.T.A. (2001) Effect of edge structure on the flux of species into forest interiors. *Conservation Biology*, **15**, 91–97.

Callaway, R.M. & Aschehoug, E.T. (2000) Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. *Science*, **290**, 521 – 523.

Chornesky, E.A., Bartuska, A.M., Aplet, G.H., Britton, K.O., Cummings-Carlson, J., Davis, F.W., Eskow, J., Gordon, D.R., Gottschalk, K.W., Haack, R.A., Hansen, A.J., Mack, R.N., Rahel, F.J., Shannon, M.A., Wainger, L.A. & Wigley, T.B. (2005) Science priorities for reducing the threat of invasive species to sustainable forestry. *BioScience*, **55**, 335–348.

Coates, A.M. (1965) *Garden shrubs and their histories*. E.P. Dutton, New York, NY USA.

Cohen, J.S. (2009). *Using Plant Traits To Understand The Impacts Of Plant Invasions on Larval Anurans*. M.S. thesis, Cornell University.

Dukes, J.S. (2001) Biodiversity and invasibility in grassland microcosms. *Oecologia*, **126**, 563–568.

Elton, C.G. (1958) *The Ecology of Invasion by Animals and Plants*. Methuen, London

Fagan, M. & Peart, D. (2004) Impact of the invasive shrub glossy buckthorn (*Rhamnus frangula* L.) on juvenile recruitment by canopy trees. *Forest Ecology and Management*, **194**, 95–107.

Galbraith-Kent, S.L. & Handel, S.N. (2008) Invasive *Acer platanoides* inhibits native sapling growth in forest understorey communities. *Journal of Ecology*, **96**, 293–302.

Gorchov, D.L. & Trisel, D.E. (2003) Competitive effects of the invasive shrub, *Lonicera maackii* (Rupr.) Herder (Caprifoliaceae), on the growth and survival of native tree seedlings. *Plant Ecology*, **166**, 13–24.

Gould, A.M.A. & Gorchov, D.L. (2000) Effects of the exotic invasive shrub *Lonicera maackii* on the survival and fecundity of three species of native annuals. *American Midland Naturalist*, **144**, 36–50.

Greipsson, S. & DiTommaso, A. (2006) Invasive non-native plants alter the occurrence of arbuscular mycorrhizal fungi and benefit from this association. *Ecological Restoration*, **24**, 236–241.

Gurevitch, J. & Padilla, D.K. (2004) Are invasive species a major cause of extinctions? *Trends in Ecology & Evolution*, **19**, 470–474.

Harrington, T.B. & Miller, J.H. (2005) Effects of application rate, timing and formulation of glyphosate and triclopyr on control of Chinese privet. *Weed Technology*, **19**, 47–54.

Hartman, K.M. & McCarthy, B.C. (2004) Restoration of a forest understory after the removal of an invasive shrub, Amur honeysuckle (*Lonicera maackii*). *Restoration Ecology*, **12**, 154–165.

Hook, D., Jr, W.M., Williams, T., Jones, S., Blaricom, D.V. & Parsons, J. (1994) Hydrologic and wetland characteristics of a piedmont bottom in SC. *Water, Air and Soil Pollution*, **77**, 293–320.

Lavergne, C., Rameau, J. & Figier, J. (1999) The invasive woody weed *Ligustrum robustum* subsp. *walkeri* threatens native forests on La Re´union. *Biological Invasions*, **1**, 377 – 392.

Lecerf, A., Dobson, M., Dang, C.K. & Chauvet, E. (2005) Riparian plant species loss alters trophic dynamics in detritus-based stream ecosystems. *Oecologia*, **146**, 432–442

Liang, K. & Zeger, S.L. (1986) Longitudinal data analysis using generalized linear models. *Biometrika*, **73**, 13–22.

Lockwood, J.L., Simberloff, D., Mckinney, M.L. & Holle, B.V. (2001) How many, and which, plants will invade natural areas? *Biological Invasions*, **3**, 1–8.

Loewenstein, N. & Loewenstein, E. (2005) Non-native plants in the understory of riparian forests across a land use gradient in the Southeast. *Urban Ecosystems*, **8**, 79–91.

MacDougall, A.S. & Turkington, R. (2005) Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology*, **86**, 42–55.

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. & Bazzaz, F.A. (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications*, **10**, 689-710.

Maerz, J.C., Blossey, B. & Nuzzo, V. (2005) Green frogs show reduced foraging success in habitats invaded by Japanese knotweed. *Biodiversity and Conservation*, **14**, 290 –2911.

Martin, P.H. (1999) Norway maple (*Acer platanoides*) invasion of a natural forest stand: understory consequence and regeneration pattern. *Biological Invasions*, **1**, 215 – 222.

Martin, P.H., Canham, C.D. & Marks, P.L. (2009) Why forests appear resistant to exotic plant invasions: intentional introductions, stand dynamics, and the role of shade tolerance. *Frontiers in Ecology and the Environment*, **7**, 142–149.

Merriam, R.W. & Feil, E. (2002) The potential impact of an introduced shrub on native plant diversity and forest regeneration. *Biological Invasions*, **4**, 369–373.

Merriam, R.W. (2003) The abundance, distribution and edge associations of six non-indigenous harmful plants across NC. *Journal of the Torrey Botanical Society*, **130**, 283–291.

Miller, J.H., Chambliss, E.B. & Oswalt, C.M. (2008) Maps of occupation and estimates of acres covered by nonnative invasive plants in southern forests using SRS FIA data posted on March 15, 2008. http://srsfia2.fs.fed.us/nonnative_invasive/Southern_Nonnative_Invasives.htm. Accessed on 1 December 2009.

Morris, L., Walck, J. & Hidayati, S. (2002) Growth and reproduction of the invasive *Ligustrum sinense* and native *Forestiera ligustrina* (Oleaceae): implications for the invasion and persistence of a nonnative shrub. *International Journal of Plant Science*, **163**, 1001–1010.

Morrison, J.A. & Mauck, K. (2007) Experimental field comparison of native and non-native maple seedlings: natural enemies, ecophysiology, growth and survival. *Journal of Ecology*, **95**, 1036–1049.

National Climatic Data Center (NCDC). (2009) Palmer hydrological drought index for the northwest division of South Carolina. http://www7.ncdc.noaa.gov/CDO/CDODivisionalSelect.jsp . Accessed 15 December 2009.

Nuzzo, V.A., Maerz, J.C. & Blossey, B. (2009) Earthworm invasion as the driving force behind plant invasion and community change in Northeastern North American forests. *Conservation Biology*, **23**, 966–974.

Osland, M.J., Pahl, J.W. & Richardson, C.J. (2009) Native bamboo [*Arundinaria gigantea* (Walter) Muhl., Poaceae] establishment and growth after the removal of an invasive non-native shrub (*Ligustrum sinense* Lour., Oleaceae): Implications for Restoration. *Castanea*, **74**, 247–258.

Oswalt, C.M., Oswalt, S.N. & Clatterbuck, W.K. (2007) Effects of *Microstegium vimineum* (Trin.) A. Camus on native woody species density and diversity in a productive mixed-hardwood forest in Tennessee. *Forest Ecology and Management*, **242**, 727–732.

Pokorny, M.L., Sheley, R.L., Zabinski, C.A., Engel, R.E., Svejcar, T.J. & Borkowski, J.J. (2005) Plant functional group diversity as a mechanism for invasion resistance. *Restoration Ecology*, **13**, 448–459.

Porcher, R.D. & Rayner, D.A. (2001) *A Guide to the Wildflowers of South Carolina*. University of South Carolina Press, Columbia, South Carolina.

Proches, S., Wilson, J.R.U., Richardson, D.M. & Rejmanek, M. (2008) Searching for phylogenetic pattern in biological invasions. *Global Ecology and Biogeography*, **17**, 5–10.

Ricciardi, A. & Cohen, J. (2007) The invasiveness of an introduced species does not predict its impact. *Biological Invasions*, **9**, 309 – 315.

Siemens, T.J. & Blossey, B. (2007) An evaluation of mechanisms preventing growth and survival of two native species in invasive Bohemian Knotweed (*Fallopia* x *bohemica* Polygonaceae). *American Journal of Botany*, **94**, 776–783.

Smith, K.E., Runion, G.B., Prior, S.A., Price, A.J., Rogers, H. & Torbert, H.A. (2008) Chinese Privet (*Ligustrum sinense*) in an elevated CO2 Environment. *Botany Research Journal*, **1**, 43 – 48.

South Carolina Exotic Pest Plant Council (SC-EPPC). (2008) Invasive Plant List. http://www.se-eppc.org/southcarolina/. Accessed on 27, December 2009.

Strauss, S.Y., Webb, C.O. & Salamin, N. (2006) Exotic taxa less related to native species are more invasive. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 5841 – 5845.

Stromayer, K.A.K., Warren, R.J., Johnson, A.S., Hale, P.E., Rogers, C.L. & Tucker, C.L. (1998) Chinese privet and the feeding ecology of white-tailed deer: the role of an exotic plant. *Journal of Wildlife Management*, **62**, 1321–1329.

Strong, C., Brown, D. & Stouffer, P. (2005) Frugivory by wintering Hermit Thrush in Louisiana. *Southeastern Naturalist*, **4**, 627–638.

Tilman, D. (1997) Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology*, **78**, 81–92.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. & Siemann, E. (1997) The Influence of functional diversity and composition on ecosystem processes. *Science*, **277**, 1300–1302.

U.S. Department of Agriculture. (2009) The PLANTS Database. http://plants.usda.gov Accessed on 27 December 2009. National Plant Data Center, Baton Rouge, LA 70874-4490 USA.

U. S. Fish and Wildlife Service. 2009. Classification of wetlands and deepwater habitats of the United States. http://www.fws.gov/wetlands/. U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C.

Vidra, R.L., Shear, T.H. & Stucky, J.M. (2007) Effects of vegetation removal on

native understory recovery in an exotic-rich urban forest. *Journal of the Torrey Botanical Society*, **134**, 410–419.

Weakley, A.S. (2008) *Flora of the Carolinas, Virginia, and Georgia, and Surrounding Areas*. http://www.herbarium.unc.edu/flora.htm. Accessed on 1 November 2009.

White, E., Vivian-Smith, G. & Barnes, A. (2009) Variation in exotic and native seed arrival and recruitment of bird dispersed species in subtropical forest restoration and regrowth. *Plant Ecology*, **204**, 231–246.

Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A. & Losos, E. (1998) Quantifying threats to imperiled species in the United States. *BioScience*, **48**, 607 – 615.

Wilcox, J. & Beck, C.W. (2007) Effects of *Ligustrum sinense* Lour. (Chinese privet) on abundance and diversity of songbirds and native plants in a southeastern nature preserve. *Southeastern Naturalist*, **6**, 535–550.

Zhang, Y., Sun, J. & Hanula, J.L. (2009) Biology and life history of *Argopistes tsekooni* (Coleoptera: Chrysomelidae) in China, a promising biological control agent of Chinese privet. *Annals of the Entomological Society of America*, **102**, 508 – 516.

CHAPTER 2

Patterns of Privet: Distribution of *Ligustrum sinense* across the Piedmont of South Carolina and causal factors.

**Abstract**

Human land use has resulted in direct and indirect changes to habitat and disturbance regimes. Riparian habitats are closely associated with human dominated systems and natural flow regime change as development and extent of impervious surfaces increases. In the southeastern United States floodplain forests are rapidly invaded by *Ligustrum sinense*, a non-native shrub, which negatively affects native plant species. The distribution of *L. sinense* appears linked to urban areas and I examined various mechanisms that may explain how development in a rapidly urbanizing area, the Piedmont of South Carolina, promotes this invasion. The results of a vegetation survey of 12 floodplain forests along an urban to rural gradient confirmed the association of *L. sinense* with watershed development and extent of impervious surfaces. I used a seedling transplant experiment along a gradient of land cover types to assess how increased development affects survival and growth of *L. sinense* and three native species. By monitoring abiotic conditions (soil nutrients, soil infiltration rates, and depth to ground water table) along with the biotic responses of the transplant seedlings I was able to infer mechanism driving *L. sinense* invasion and the demise of native vegetation.

Watershed development ranged from 1 to 45 (%) but did not affect abiotic conditions, thus watersheds showed no disturbance gradient, and there were only modest differences in soil nutrients, soil infiltration rates, and ground water depths. Growth and survival of *L. sinense* did not differ between watersheds and was not related to watershed development. Native species were able to survive at all sites, but at lower

rates than *L. sinense* and suffered more herbivory than *L. sinense* seedlings. These results indicate that *L. sinense* is a strong invader that does not need disturbance events to invade habitats.

Surveys of the size of *L. sinense* in the different watersheds provided insights into the factors promoting *L. sinense* distribution. Maximum DBH was positively correlated with *L. sinense* abundance and cover and had the highest explanatory power. Since growth and survival of *L. sinense* was similar between watersheds, this means that sites with large *L. sinense* individuals were the earliest invaded. The species traits of *L. sinense* allow it to invade all floodplain forests and the correlation with watershed development is a consequence of historical sources of propagules. This highlights the importance of reducing exotic horticultural imports to new areas and encouraging native landscaping. With this information land managers need to plan for protecting critical habitat no matter its spatial relation to urban areas.

**Introduction**

Human influences shape the vast majority of earth's surface and humans currently are the world's greatest evolutionary force (Palumbi 2001). Expansion and intensification of agriculture leads to increases in nutrient runoff and eutrophication of coastal waterways (Howarth et al. 1996). Rapid urbanization alters ecosystem processes in areas with high biodiversity (Cincotta, Wisnewski, & Engleman 2000) and is persistent in the landscape (McKinney 2002). With more than half the world's population now living in cities (Grimm, Faeth, et al. 2008) the urban footprint reaches far beyond the suburbs and may reduce native and increase non-native species richness (McKinney 2008) as urbanization is a major vector for the introduction of invasive species (Vitousek et al. 1997). Development increasing the extent of impervious surfaces changes water flow regimes (i.e., flashier streams), increase

stream incision, alter channel geomorphology, and lower ground water tables far beyond city limits (Poff et al. 1997). This is collectively called the "urban stream syndrome" (Walsh et al. 2005) and it can lead to hydrologic drought in associated riparian wetlands(Groffman et al. 2003).

Changes to natural disturbance regimes are considered important mechanisms facilitating establishment and spread of invasive species (Dukes & Mooney 1999). However, disturbances are difficult to classify and include flooding, fire, insect outbreaks and many other forces; they have different frequencies and differ in magnitude. There are few ecosystems on earth that are not at least occasionally affected by catastrophic disturbances. All species are frequently exposed to disturbance events so it is not immediately obvious why disturbance should favor introduced species unless disturbance regimes are qualitatively or quantitatively novel. In fact introduction of invasive species itself can be considered a disturbance event, for example the introduction of grazers, earthworms or predators into areas where these taxa or functional groups did not exist previously. There is evidence to suggest disturbance facilitates invasions and that without habitat disturbance (King & Tschinkel 2008) or alteration of natural disturbance regimes (MacDougall & Turkington 2005) invasive species have minimal effects on diversity or abundance of native species. Disturbance can increase propagule pressure by facilitating spread (Cadenasso & Pickett 2001; McDonald & Urban 2006). Increases in propagules are a key factor for promoting invasibility of habitats (Levine 2001, Van Holle & Simberloff 2005). However, invasions are also often facilitated by lack of top-down control, commonly called the Enemy Release Hypothesis, ERH (Keane & Crawley 2002, Carpenter & Cappuccino 2005). The ERH is based on some fundamental assumptions that population regulation is influenced by natural enemies and absence of herbivory results in increased local abundance and range expansion. Success of

biological control programs (Crawley 1989) in suppressing host species without change in disturbance regimes offers strong support for regulatory effectiveness of natural enemies and questions the importance of disturbance as driver of biological invasions. Another factor independent of disturbance is species traits of invasives that result in competitive superiority over native species. Some non-native species may be pre-adapted to become invasive due to evolutionary history and habitat specificity (Brown & Sax 2000). In particular habitats, certain species' traits confer advantages to non-native species, for example drought tolerance in deserts or height in wetlands, but often these traits are not generalizable to other habitats. Also species with traits different from the recipient community are functional distinct and more likely to invade (Dukes 2001). Understanding the relative importance of these mechanisms in promoting invasive species will help answer the question of whether invasive species are the drivers or passengers in the demise of many native species (Didham et al. 2005; MacDougall & Turkington 2005).

*Ligustrum sinense* Loureiro (Chinese Privet) arrived in North America from Asia in the 1850s and is commonly used as a hedge plant due to its shrub like life form and vigorous growth (Coates 1965). A member of the Oleaceae family, there are no native members of the genus *Ligustrum* in North America (Weakly 2008). *Ligustrum* species have invaded an estimated 1.09 million forested hectares (Miller, Chambliss, & Oswalt 2008) in the southeastern United States, largely in riparian habitats (Merriam 2003). Dense *L. sinense* stands are associated with reduced native plant growth and survival (Osland, Pahl, & Richardson 2009) and *L. sinense* is considered an invasive species in many states, including South Carolina where it is listed as a severe threat (SC-EPPC 2008). Urbanization appears correlated with increased *L. sinense* abundance (Burton, Samuelson, & Pan 2005; Loewenstein & Loewenstein 2005; Burton & Samuelson 2008), although mechanisms for increased survival, growth or

dispersal are unclear. While no studies have examined the longevity of *L. sinense* individuals, stands of *L. sinense* have been documented to persist for more than 40 years in the invaded range (Ward 2002). *Ligustrum sinense* has high rates of reproduction with an average of 1300 fruits per square meter of *L. sinense* canopy (Westoby, Dalby, & Adams-Action 1983) and germination rates up to 65% (Panetta 2000). The seeds are bird dispersed (Strong, Brown, & Stouffer 2005) and fruits can float in water for up to two weeks (Greene, Personal Observations) allowing for effective dispersal in floodplain forests. Seedlings and established plants can tolerate both flooding and low light conditions (Brown & Pezeshki 2000) and mature plants can reach a height of 9 m and occupy a near vacant shrub niche that is not filled by native species in the mid canopy. In the southeastern United States *L. sinense* is evergreen (Miller 2003) and has low rates of both leaf herbivory and leaf abscission (Morris, Walck, & Hidayati 2002).

This study took place in the Piedmont ecoregion of South Carolina, an area characterized by rolling hills and streams with associated floodplain forests. Piedmont floodplain forests are wetlands distinguished by periodic flooding of the adjacent streams (Hook et al. 1994) that can leave the area inundated with standing water for up to five days (B.T.Greene, Personal Observations). Land use history include intense cotton farming from 1820 to 1930 and dramatic soil erosion (Lockaby 2009) until abandoned fields reverted to forests, increasing forest cover in some areas up to 30% by 1967 (Trimble, Weirich, & Hoag 1987). However, rapid population growth and land development increased urban land cover in the eastern Piedmont ecoregion (parts of Virginia, North Carolina, South Carolina, Georgia, and Alabama) from 11.9 % to 16.4% and exurban development in the Piedmont of South Carolina increased by 50% from 1973 to 2000 (Brown et al. 2005). Development is the leading cause of wetland

loss (often floodplain forests) in the southeastern US (Faulkner 2004) with a projected 45% growth rate from 2000 to 2030 (Grimm, Foster, et al. 2008).

Floodplain forests are wetlands that have a distinct Piedmont plant community (Cowell 1993) and are response driven systems that serve as integrators of their watershed. A natural flow regime has been identified as a critical element for maintaining ecosystem health in these aquatic-terrestrial systems (Poff et al. 1997) yet changes in land cover alter flow regimes (Poff, Bledsoe, & Cuhaciyan 2006). Piedmont streams in urban watersheds have flashier hydrographs with more frequent elevated peak discharges (Schoonover, Lockaby, Helms 2006) and are a local example of altered flow regimes.

These characteristics make the Piedmont ecoregion of South Carolina ideally suited to investigate potential causal relationships between land use, invasive species distributions, and mechanisms causing the demise of native plant species in invaded ecosystems. Different theories attempt to explain the mechanisms that provide invasive species advantages over native species. The contending theories of disturbance assistance, competitive advantage, and enemy release have different ultimate causes that require unique management strategies to address. My study explored the relative importance of these different hypotheses to explain the prevalence and distribution of *L. sinense*. The first part of this study examined if *L. sinense* prevalence was related to development in the watershed. Based on previous research, I predict that (1) abundance and cover of *L. sinense* will increase with percent watershed development. If this relationship is true the next step is to identify the mechanism promoting *L. sinense* invasion. If disturbance is important than (2) abiotic properties should differ between watersheds and (3) growth and survival of *L. sinense* will be greater in developed watersheds as compared to more forested watersheds. If species traits of *L. sinense* are the dominant mechanism, than (4)

growth and survival of *L. sinense* should not differ between watersheds and (5) herbivory and growth rates should differ from native species giving *L. sinense* a competitive advantage.

**Methods**

SITE SELECTION

I used the 2001 National Land Cover Database (Homer et al. 2004) and the National Wetland Inventory (USFWS 2009) to initially select palustrine forested wetlands in watersheds across a gradient of urban to rural to forested land cover. I visited all potential sites in late May 2007 and rejected sites with livestock grazing, sites that had been recently logged, or sites with floodplains less than 100 m wide. I chose 12 hydrologically independent floodplain forests and their associated watersheds for the study (Figure 2-1).

All sites are secondary hardwood forests with a canopy dominated by *Acer negundo* L., *Fraxinus pennsylvanica* Vahl, *Celtis laevigata* Willd., *Platanus occidentalis* L., and *Populus deltoides* Marsh. Native shrubs such as, *Ilex decidua* Walter, *Asimina triloba* (L) Dunal, *Carpinus caroliniana* Walter, and *Arundinaria tecta* (Walter) Muhlenburg are common, but sparsely distributed. Grasses and sedges dominate the herbaceous understory. All sites showed signs of deer (*Odocoileus virginianus*) presence (browse, trails, and rubs) and non-native earthworms (castings and individuals). The region has a warm-humid temperate climate type with a mean annual temperature of 15.8°C and mean annual precipitation of 116 cm, but the region experienced a drought for the entire time of this study as indicated by the Palmer Hydrologic Drought Index (NCDC 2009). Sites were a mix of both public (local parks and US Forest Service) and private lands (Table 2-1).

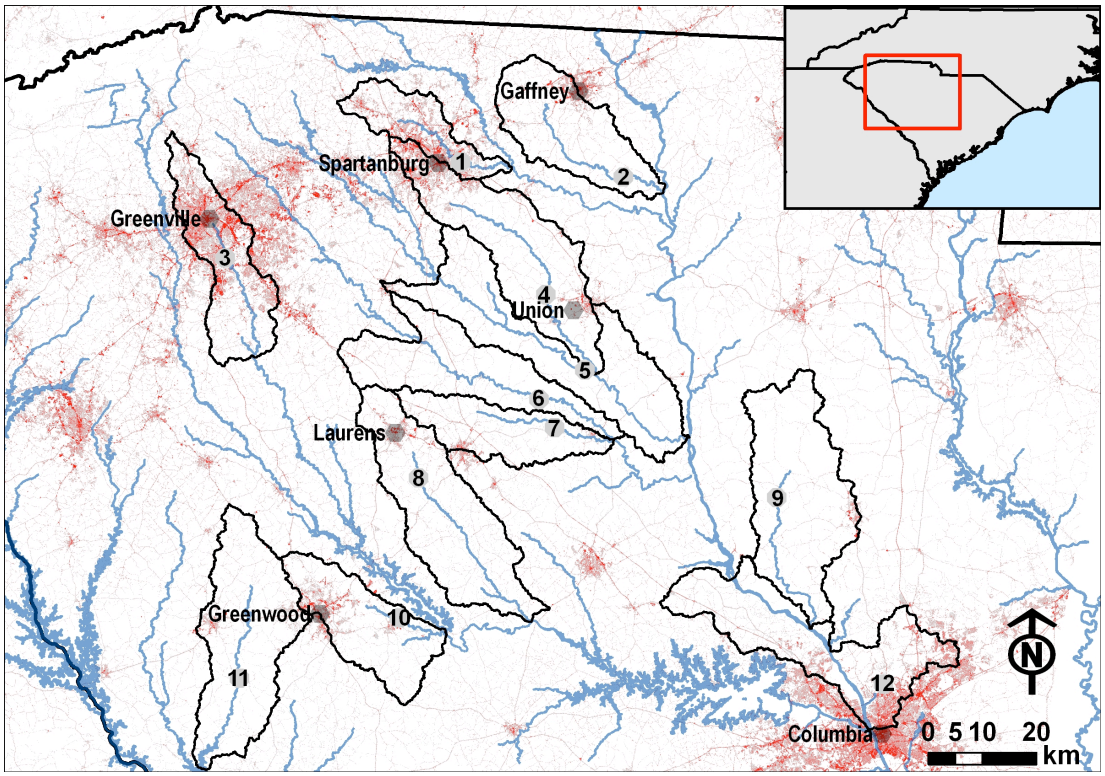

Figure 2-1 Field site locations and their associated streams (blue), watersheds (black), and major cities (grey hexagons) in the Piedmont ecoregion of South Carolina. Background is a 2001 NLCD datalayer for impervious surfaces, where red background indicates high amounts of impervious surfaces. Sites: Lawson's Fork Creek (1), Thicketty Creek (2), Reedy River (3), Fairforest Creek (4), Tyger River (5), Enoree River (6), Duncan Creek (7), Little River—Laurens County (8), Little River – Fairforest County (9), Wilson's Creek (10), Long Cane Creek (11), Crane Creek (12). Sites 1-9 were sites used for the transplant experiment.

## LAND COVER ANALYSIS

I conducted land cover analysis with Arc GIS v9.2 (ESRI 2007) using land cover, forest, and impervious surfaces data layers obtained from the 2001 National Land Cover Database. Land cover classification followed Homer et al. (2004) with classes 21-24 pooled for development, 41-43 for forest, and 90-99 for wetlands. I measured direct distance and flow path distance from the field sites to the nearest developed area in kilometers. To be identified as a developed area, land use categories were aggregated into 36 hectare grids and classified as developed if more than half the cells inside the grid contained a developed land cover class. I used watershed level

hydrologic units (HUC 10) obtained from the Watershed Boundary Dataset (USDA-NRCS 2007) for watershed delineation. I grouped watersheds by percent development into four categories (three urban watersheds, two developing watersheds, four mixed watersheds and three forested watersheds) representing the different dominant land cover patterns (Table 2-2).

Table 2-1 Table of sites with land ownership and location data

| Name | Code | Ownership | Latitude (N) | Longitude (W) |
|---|---|---|---|---|
| Crane Creek | CC | Private – Timber | 34°05'00" | 81°01'49" |
| Duncan's Creek | DC | Public – USFS | 34°30'39" | 81°41'42" |
| Enoree River | ER | Public – USFS | 34°33'20" | 81°43'33" |
| Fairforest Creek | FC | Private – Timber | 34°43'48" | 81°42'43" |
| Long Cane Creek | LC | Public – USFS | 34°05'08" | 82°19'18" |
| Lawson's Fork Creek | LF | Public – Nature Preserve | 34°57'05" | 81°53'20" |
| Little River | LL | Private – Personal Property | 34°25'24" | 81°57'58" |
| Little River | LR | Private – Personal Property | 34°23'37" | 81°14'56" |
| Reedy River | RR | Public – Nature Preserve | 34°47'15" | 82°21'43" |
| Thicketty Creek | TC | Private – Timber | 34°55'39" | 81°33'19" |
| Tiger River | TR | Public – USFS | 34°36'20" | 81°38'05" |
| Wilson's Creek | WC | Private – Personal Property | 34°11'21" | 82°00'04" |

VEGETATION SURVEY

I surveyed all 12 field sites for vascular plants during the peak of the growing season from 11 June to 15 July 2007. At each site, except Lawson's Fork and Reedy River (sites 1 and 2 respectively, Figure 2-1), I selected a 200 m stream reach at least 75 m from the nearest forest edge. At Lawson's Fork and Reedy River I used a 100 m stream reach to ensure contiguous habitat. At all sites I randomly located five transects along this reach. Each transect ran along a compass heading perpendicular to the stream and extended 100 m into the floodplain interior. Along each transect, I

Table 2-2 Sites and the percent land cover in their associated watershed. All data based on 2001 National Land Cover Database data.

| Site | Category | Map # | Developed (%) | IS (%) | Forest (%) | Agriculture (%) |
|---|---|---|---|---|---|---|
| **ER** | Forest | 6 | 1.2 | 0.8 | 65.0 | 17.5 |
| **LR** | Forest | 9 | 4.0 | 0.6 | 75.1 | 7.0 |
| **TR** | Forest | 5 | 4.7 | 0.5 | 72.7 | 12.1 |
| **LC** | Mixed | 11 | 7.4 | 0.8 | 68.7 | 13.3 |
| **LL** | Mixed | 8 | 8.2 | 1.1 | 61.5 | 19.2 |
| **DC** | Mixed | 7 | 9.5 | 1.5 | 69.6 | 12.1 |
| **TC** | Mixed | 2 | 9.6 | 1.9 | 57.6 | 22.4 |
| **WC** | Developing | 10 | 15.9 | 2.8 | 57.2 | 16.4 |
| **FC** | Developing | 4 | 17.0 | 4.1 | 58.5 | 13.9 |
| **CC** | Urban | 12 | 21.4 | 5.2 | 62.4 | 6.6 |
| **LF** | Urban | 1 | 38.9 | 9.5 | 35.7 | 19.7 |
| **RR** | Urban | 2 | 44.5 | 13.7 | 32.8 | 15.5 |

| Site | Wetland (%) | Direct Distance (km) | Flow Distance (km) | Area (ha) |
|---|---|---|---|---|
| **ER** | 3.4 | 10.5 | 34.9 | 48059 |
| **LR** | 2.8 | 9.3 | 20.9 | 62886 |
| **TR** | 3.4 | 9.5 | 47.5 | 63420 |
| **LC** | 1.7 | 8.5 | 12.5 | 59112 |
| **LL** | 3.0 | 6.2 | 8.6 | 59587 |
| **DC** | 3.4 | 6.4 | 20.8 | 31079 |
| **TC** | 1.6 | 14.7 | 28.1 | 40807 |
| **WC** | 2.8 | 1.3 | 5.4 | 37242 |
| **FC** | 4.0 | 2.1 | 30.9 | 56560 |
| **CC** | 3.0 | 0.3 | 0.7 | 60183 |
| **LF** | 2.1 | 0.3 | 0.8 | 22034 |
| **RR** | 2.8 | 0.1 | 1.0 | 39106 |

randomly located six plots to measure plant composition (N= 30 plots/site). I nested a $1m^2$ area (herbaceous plot) inside a 2x5m grid (shrub plot) where I identified, counted all stems and visually estimated herbaceous cover (%) for each species. In addition, I recorded height of the tallest plant in each corner and then created a mean maximum herbaceous height. Not all plants had identifiable characteristics during the survey period so some species were grouped by genus using identical groupings at all sites. I used the $10m^2$ area to identify, count all individuals, and visually estimate cover (%) for each shrub species. The shrub level included both woody and herbaceous plants that were taller than the mean maximum herbaceous height, but did not reach above 8 m total height.

FOREST STAND MEASUREMENTS

I used the same transect headings and locations from the vegetation survey to collect forest stand measurements from August to October 2008. I established a 2m wide by 100 m long belt transect and identified and measured all woody stems at least 1.5 cm in diameter at breast height (DBH) for each of the five transects per site covering a total area of 1000 $m^2$. For individuals with multiple stems I recorded the largest stem diameter.

TRANSPLANT EXPERIMENT

To assess performance of native and introduced species in different floodplain forests I used *L. sinense*, *A. negundo* L. var. *negundo, Chasmanithum latifolium* (Michaux) Yates and *Allium canadense* L. var. *canadense*. These species represent different life forms and life histories but are very common in my study sites. The introduced *L. sinense* achieves the highest biomass of any invasive species in the floodplain forest community (B. Greene, unpublished data); A. *negundo* is a common native floodplain

tree while *C. latifolium* is a common understory grass; *A. canadense* is a common early season forb found in many habitats across the eastern United States.

I collected seeds for *A. canadense* in May 2007 and for the remaining species in the fall and winter of 2007-2008. I stored *A. canadense, C. latifolium* and *L. sinense* seeds dry at 22˚C in paper bags and *A. negundo* seeds in the dark at 5˚C in plastic bags with moist paper towels. In mid-March 2008 I scattered seeds on a moist 50:50 mixture of Pro-Mix potting soil (Farfard Canadian growing mix No. 1-P, Agawam, Massachusetts, USA) and playground sand in plastic trays in a greenhouse maintained at 25˚C with a 12 hr photoperiod. I watered trays periodically from above to maintain surface moisture for the developing seedlings. After nine weeks I selected 180 individuals of similar size from each species. All species except for *A. negundo* had sufficient seeds germinate to provide seedlings for the experiment. As a replacement, I collected 4-leaved *A. negundo* seedlings on 26 April 2008 at Lawson's Fork Creek. I also collected *L. sinense* naturally recruited seedlings on 27 April 2008 at Little River Laurens to compare field-grown plants for the two woody species in my experiment. From my vegetation survey sites, I selected three field sites each with predominant urban, mixed, and forested land cover. At each site I established a transplant garden consisting of 80 1 x 1 m cells. Each grid consisted of two adjoining rows of 10 cells separated by a 1m wide walkway from the next two adjoining rows for a total of eight rows. Each grid was located in the floodplain forest away from mature *L. sinense* sub-canopy. I divided individuals of each transplant species randomly into groups of 20. I selected an individual at random from this group and planted it bare root into the center of a cell directly into the extant vegetation. To avoid immediate plant competition to affect transplants, I anchored a 20 x 20 cm black plastic sheet (6mm) to the substrate using metal nails. Each plastic sheet contained a 25cm$^2$ center hole where the seedling was planted. I marked all seedlings individually with a numbered metal

ID tag to ensure proper identification on subsequent visits. Plastic sheets were quickly overgrown by vegetation but made relocation much easier. The local vegetation matrix was representative of the floodplain forest herbaceous community, dominated by grasses and sedges, and included both native and non-native species.

I planted 20 individuals of each species at each site (total = 720 individuals) from 27 April 2008 to 1 May 2008. I replaced dead individuals that most likely died due to transplant shock only on the first subsequent visit after one week but replaced no further individuals in subsequent weeks. I watered plants twice, once upon planting and again at the first re-visit. During the first growing season I monitored sites weekly for the first month and then every other week in June and July, once in mid-August, and once in late October (10 sample periods over 27 weeks). In the second growing season I visited each site once in February, May, July, and October (4 sample periods over 49 weeks) to measure plant growth and to record survival and herbivory. I counted individuals as alive if green photosynthetic tissue was present. I measured height (to 0.5 cm accuracy) to the apical meristem for *A. negundo* and *L. sinense* and to the height leaves reached when held erect for *A. canadense* and *C. latifolium* . I recorded the presence or absence of stem and leaf herbivory qualitatively. When I terminated the experiment and removed all plants in October 2009, I had recorded seedling survival and growth on a total of 14 sampling dates over a period of 76 weeks.

ABIOTIC MEASUREMENTS

I measured soil infiltration, soil nutrients, and ground water table distance from surface to assess if differing land covers of each watershed resulted in differences in abiotic conditions at my research sites. I measured soil infiltration capacity using a double ring infiltrometer (65 cm and 40 cm diameter) at each site between 17 July

2007 and 7 August 2007. At each site I randomly selected 10 vegetation plots to measure the local soil infiltration capacity. At each test location the two metal rings would be driven at least five centimeters into the ground and then both filled with a known volume of water and timed in seconds to measure how long it took for all the water in the inner ring to infiltrate. This would be done twice in a row at each location and the second measurement was used for analysis of the saturated soil infiltration capacity (liters/second).

I installed seven ground water table wells in June 2008 at each of the nine transplant sites. I randomly choose two transects from the vegetation survey and placed one well at 15 m, 50 m, and 100 m from the stream and an additional one adjacent to the transplant grid. Each well consisted of a 3m long PVC pipe (3.8 cm diameter) with 1cm diameter holes drilled every 10cm along 2.6m of the pipe and then 2.75m of the pipe was wrapped in cheesecloth to prevent sedimentation. I used a hand held soil auger (5cm diameter), to drill a hole to a depth of 2.75 m below the soil surface and installed the wells leaving 0.25 m of the pipe above ground. I refilled the holes initially with sand and then packed the top 15 cm with clay. I capped wells to prevent water entering from above. I measured the distance to the water table 10 times from June 2008 to May 2009 by blowing air into a thin plastic tube while lowering it into the well until I heard bubbles. I then measured the tube length below ground to record water table depth. During this time period the water table dropped below the depth of 2.75 m for some water wells and for analysis 2.75 m was substituted for the value. I collected soil for nutrient analysis from each of the nine field sites used for the transplant experiment in February 2009. I removed the upper 10 cm of a soil core (10cm in diameter) at three locations directly adjacent to transplant gardens. I combined and thoroughly mixed samples which I then submitted to the Cornell Nutrient Analysis Laboratory.

## STATISTICAL ANALYSIS

I compared land cover of the different watershed categories using ANOVA followed by multiple pairwise comparisons using Tukey's HSD test. I examined relationships between *L. sinense* abundance and cover to land cover and forest stand measurements using linear regression. I used a linear mixed effect model with site as a random effect to analyze results of relative growth rate and herbivory between species from the transplant experiment for each sampling period using Holm – Bonferroni correction to account for the multiple comparisons. I analyzed survival and maximum growth data from the transplant experiment using linear regression, ANOVA and Tukey's HSD. I created survival curves for each species at each site and analyzed final survival by site using a binomial Generalized Linear Model. I calculated maximum growth as the greatest increase in height from the initial height of surviving individuals for each growing season. I used the Mann – Whitney test to compare maximum growth rates of all living *A. negundo* and *L. sinense* for both growing seasons.

I report transplant experiment data for two growing seasons (27 April to 30 October 2008 and 31 October 2008 to 10 October 2009). I analyzed *A. candense* survival rates for the second growing season from week 53 because at the final sampling date (10 October 2009) plants were still dormant. I compared soil infiltration rates by site using ANOVA and Tukey's HSD. I examined correlations between soil nutrients and plant species growth using linear regression. To avoid pseudoreplication, I used a derived variable analysis for comparing the mean water table depth by site with ANOVA and Tukey's HSD. I inspected normality and homoscedasticity with both graphical and statistical methods to ensure test assumptions were met. In cases where data was non-normally distributed I used log10 transformations. I conducted all analyses using R (R Development Core Team 2008).

**Results**

LAND COVER AND FOREST STAND RELATIONSHIPS

Planned site selection resulted in strong gradients of land cover, which enabled comparisons among replicate watersheds. My site categories are distinct for development ($F_{3,8} = 15.64$, $P = 0.001$), impervious surfaces ($F_{3,8} = 10.72$, $P = 0.004$), forests ($F_{3,8} = 4.82$, $P = 0.03$), direct distance from urbanization ($F_{3,8} = 11.93$, $P = 0.003$) and flow path distance from urbanization ($F_{3,8} = 4.97$, $P = 0.03$) (Table 2-3). . There was no difference among watershed categories for agriculture and wetland land cover or watershed area and I omitted these cover types from my subsequent analyses. I classified Fairforest Creek as an urban watershed for my transplant experiment since developing watersheds showed large similarities with urban ones and I needed to use this site for logistical reasons.

The mean *L. sinense* cover increases as development ($R^2 = 0.55$, $P = 0.006$) and impervious surfaces ($R^2 = 0.49$, $P = 0.01$) increase (Figures 2-2 & 2-3). In contrast, *L. sinense* cover decreases as direct distance to developed areas ($R^2 = 0.50$, $P = 0.01$), and flow path distance to developed areas ($R^2 = 0.49$, $P = 0.01$) increases (Figures 2-4 & 2-5). An increase in forest cover of a watershed was associated with a decrease in *L. sinense* cover ($R^2 = 0.57$, $P = 0.005$; Figure 2-6). None of the land cover types had a significant correlation to abundance of *L. sinense* (development: $R^2 = 0.23$, $P = 0.12$; impervious surfaces: $R^2 = 0.21$, $P = 0.13$; forest: $R^2 = 0.31$, $P = 0.06$; direct distance; $R^2 = 0.18$, $P = 0.17$; flow path distance: $R^2 = 0.05$, $P = 0.48$).

As *L. sinense* DBH increased (Figures 2-7 & 2-8) *L. sinense* abundance ($R^2 = 0.43$, $P = 0.02$) and mean cover ($R^2 = 0.37$, $P = 0.04$) increased as well. I also found a significant relationship between the number of mature *L. sinense* individuals with a DBH over 5cm and total *L. sinense* abundance ($R^2 = 0.48$, $P = 0.01$) and a highly

Table 2-3 Mean watershed values (± 1 S.E.) for each of the four watershed categories. Groups with different letters in a column are significantly different based on a Tukey Post Hoc test. Data in developed and impervious surfaces (IS) cover types were log10 transformed to meet the assumptions of normality for the ANOVA.

| Watershed Category | Developed | I.S. | Direct | Flow |
|---|---|---|---|---|
| Forest | 3.3 ± 1.1[a] | 0.6 ± 0.1[a] | 9.8 ± 0.4[a] | 34.4 ± 7.7[a] |
| Mixed | 8.7 ± 0.5[b] | 1.3 ± 0.2[ab] | 8.9 ± 2.0[a] | 17.5 ± 4.4[ab] |
| Developing | 16.5 ± 0.5[bc] | 3.4 ± 0.6[bc] | 1.7 ± 0.4[b] | 18.2 ± 12.8[ab] |
| Urban | 35.0 ± 7.0[c] | 9.5 ± 2.4[c] | 0.2 ± 0.1[b] | 0.8 ± 0.1[b] |

| Watershed Category | Forest | Agriculture | Wetland | Area |
|---|---|---|---|---|
| Forest | 70.9 ± 3.0[a] | 12.2 ± 3.0 | 3.2 ± 0.2 | 58122 ± 5034 |
| Mixed | 64.4 ± 2.9[ab] | 16.8 ± 2.4 | 2.4 ± 0.5 | 47646 ± 9659 |
| Developing | 57.8 ± 0.6[ab] | 15.1 ± 1.2 | 3.4 ± 0.6 | 46901 ± 9659 |
| Urban | 43.6 ± 9.4[b] | 13.9 ± 3.9 | 2.7 ± 0.3 | 40441 ±11033 |

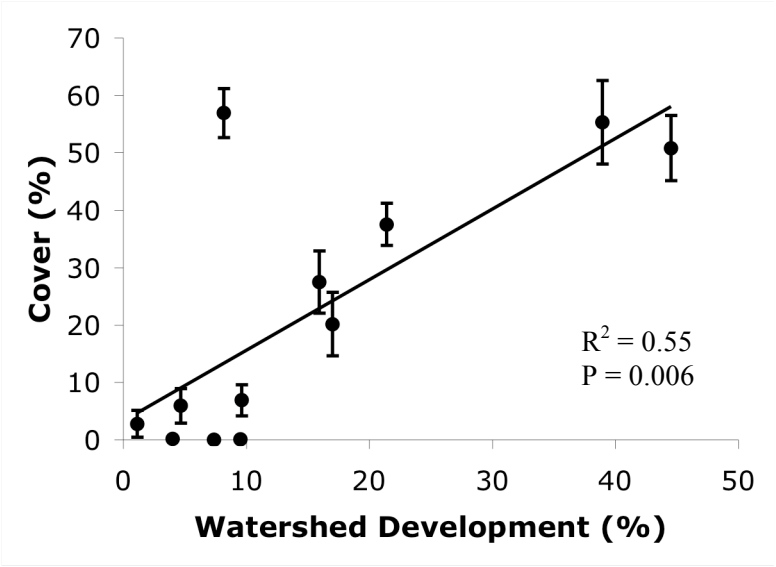


Figure 2-2 The cover of *L. sinense* (%) as a function of watershed development (%). Data are means ± 1 SE from 12 field sites (30 plots per site).

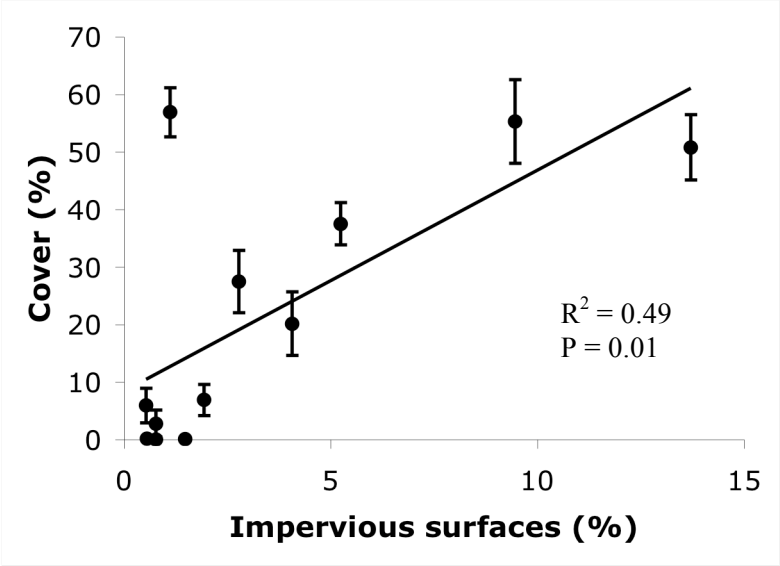


Figure 2-3 Cover of *L. sinense* (%) as a function of impervious surfaces (%). Data are means ± 1 SE from 12 field sites (30 plots per site).

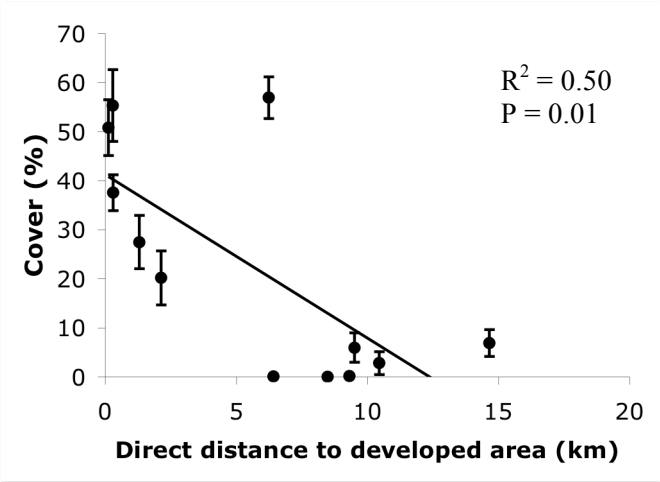


Figure 2-4 The cover of *L. sinense* (%) as a function of direct distance to developed area (km). Data are means ± 1 SE from 12 field sites (30 plots per site).

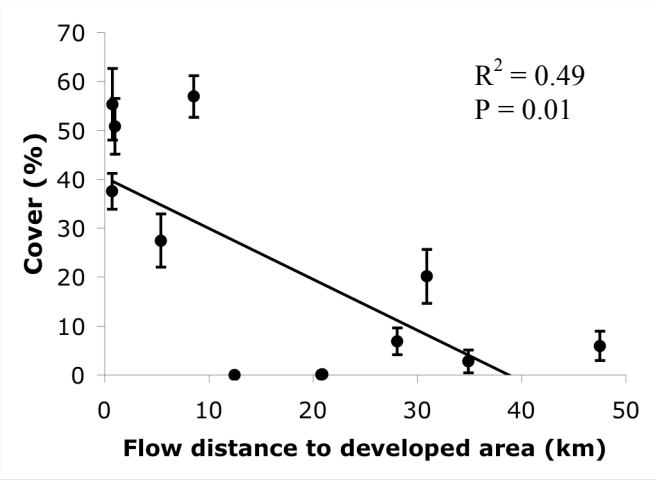


Figure 2-5 The cover of *L. sinense* (%) as a function of flow distance to developed area (km). Data are means ± 1 SE from 12 field sites (30 plots per site).

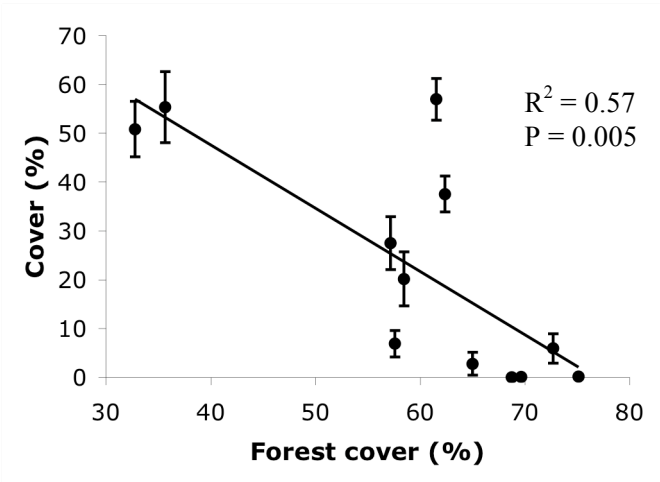


Figure 2-6 The cover of *L. sinense* (%) as a function of forest cover (%). Data are means ± 1 SE from 12 field sites (30 plots per site).

significant relationship for mean *L. sinense* cover ($R^2 = 0.71$, P = 0.0006, Figures 2-9 & 2-10). I found the best correlation and thus highest explanatory power between the maximum *L. sinense* DBH at each site and *L. sinense* abundance ($R^2 = 0.52$, P = 0.007) and *L. sinense* cover ($R^2 = 0.76$, P = 0.0002, Figures 2-11 & 2-12). I found no significant relationships of *L. sinense* abundance ($R^2 = 0.10$, P = 0.32) or mean cover ($R^2 = 0.04$, P = 0.53) with native tree DBH.

ABIOTIC MEASUREMENTS

Differences in soil infiltration rates among field sites were significant ($F_{11, 109} = 2.52$, P = 0.007), but were entirely driven by differences between the developing Wilson's Creek and the forested Little River Fairfield (P = 0.049) sites (Figure 2-13). I analyzed infiltration rates using sites grouped by watershed categories ($F_{3,117} = 3.11$, P = 0.03; Figure 2-14), but only differences between forest and mixed sites were significant. For mean depth to water table, differences among sites were significant ($F_{8,79} = 0.692$, P = 0.01), but none of the pairwise comparisons of sites were significantly different (Tukey HSD; Figure 2-15).

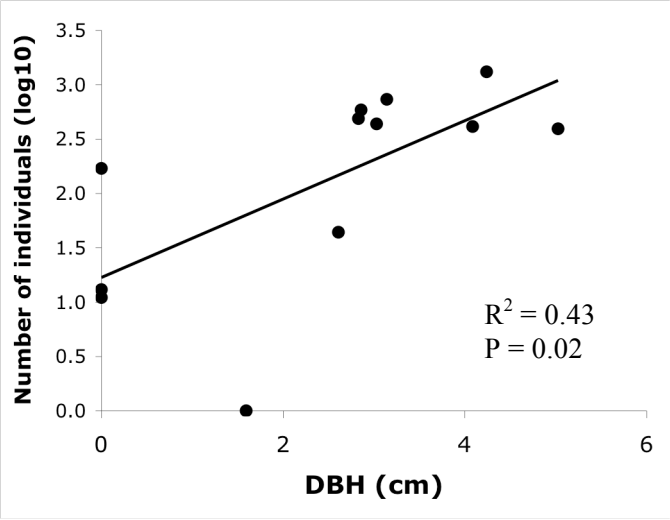


Figure 2-7 Number of *L. sinense* individuals (log10 transformed) as a function of mean *L. sinense* DBH (cm). Data are totals from 12 sites (30 plots/site).

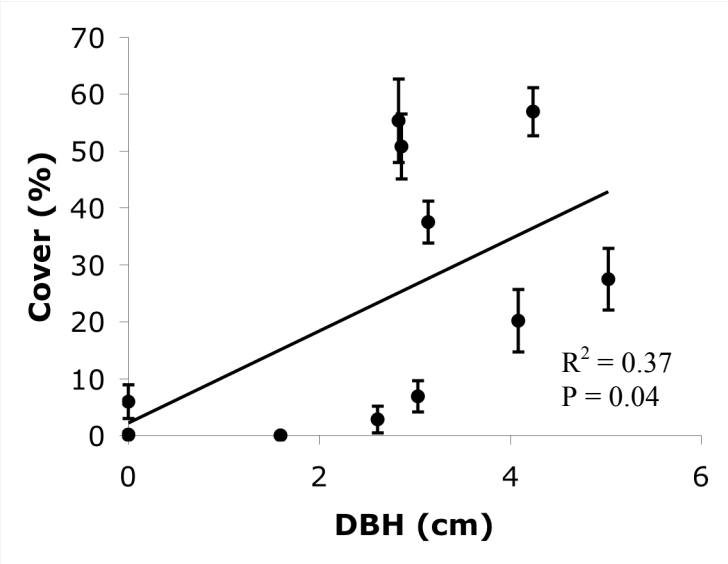


Figure 2-8 The cover of *L. sinense* (%) as a function of mean *L. sinense* DBH (cm). Data are means ± 1 SE from 12 field sites (30 plots per site).

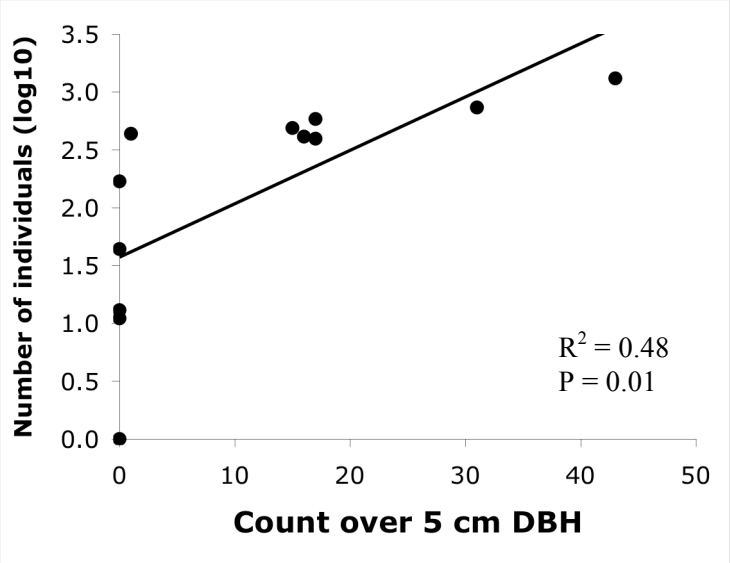


Figure 2-9 Number of *L. sinense* individuals (log10 transformed) as a function of count of *L. sinense* individuals with a DBH > 5 cm. Data are totals from 12 sites (30 plots/site).

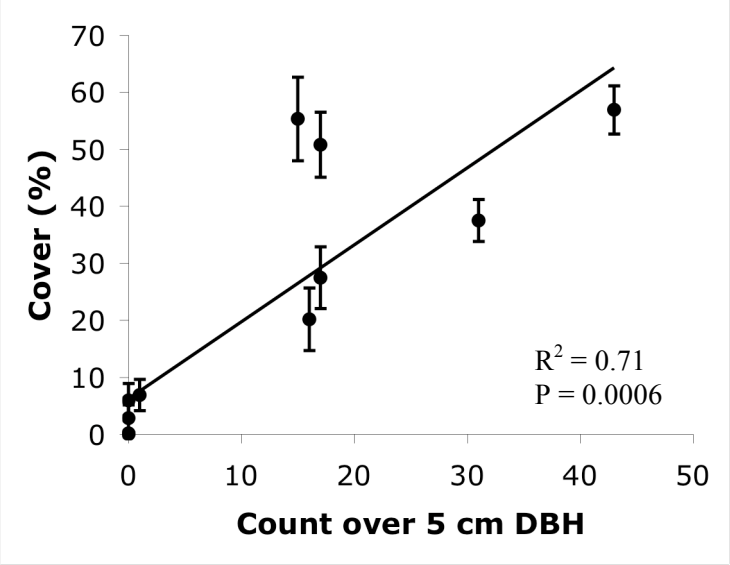


Figure 2-10 The cover of *L. sinense* (%) as a function of count of *L. sinense* individuals with a DBH > 5 cm. Data are means ± 1 SE from 12 field sites (30 plots/site).

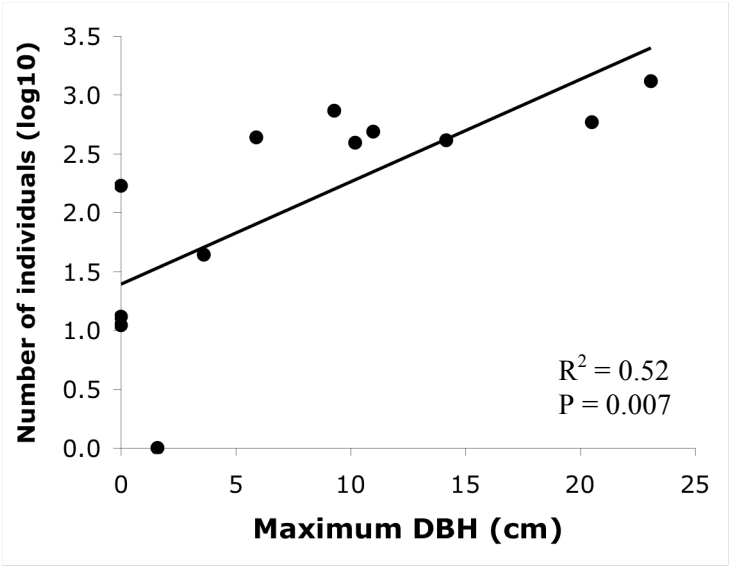


Figure 2-11 Number of *L. sinense* individuals (log10 transformed) as a function of the maximum *L. sinense* DBH at each site. Data are totals from 12 sites (30 plots/site).

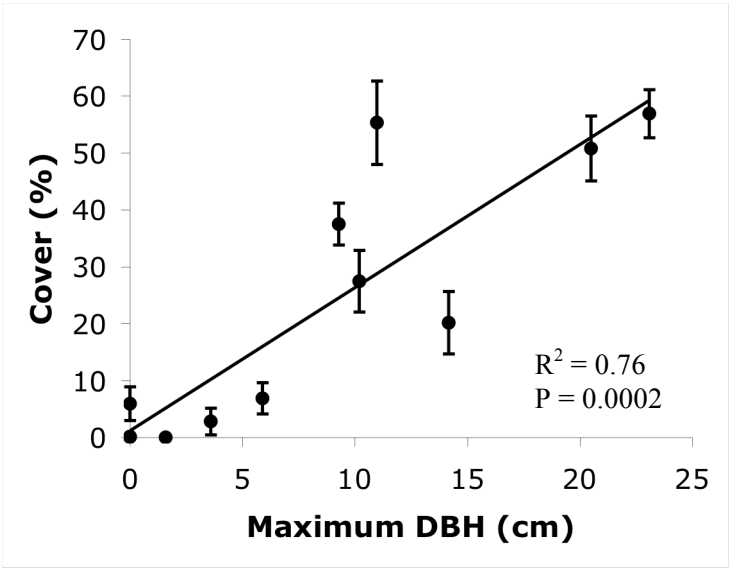


Figure 2-12 The cover of *L. sinense* (%) as a function of the maximum *L. sinense* DBH at each site. Data are means ± 1 SE from 12 field sites (30 plots/site).

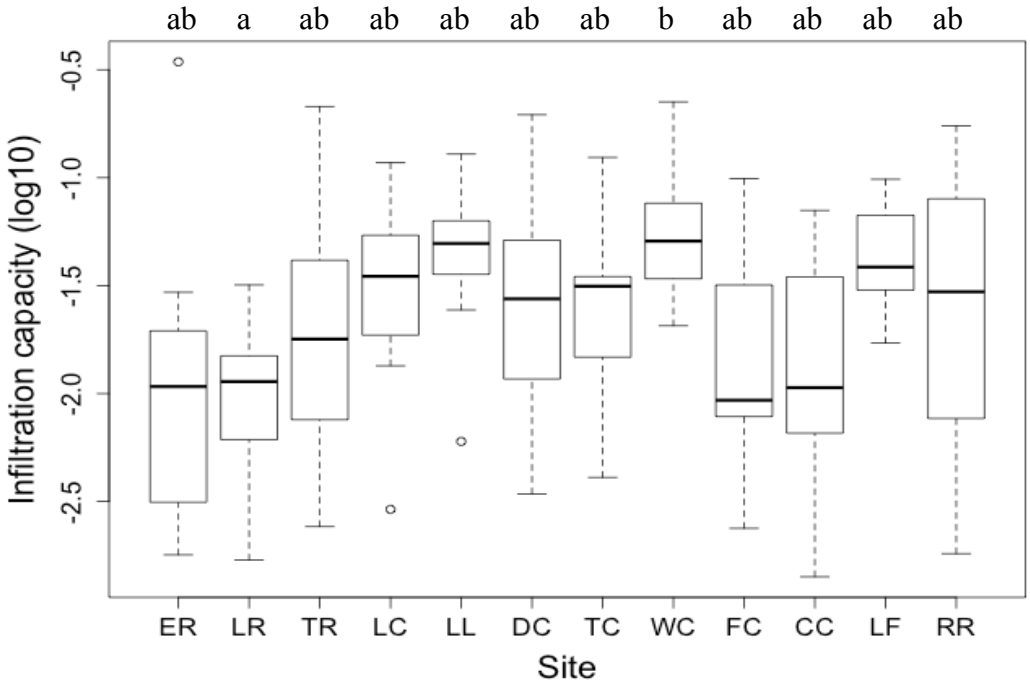


Figure 2-13 Boxplot of soil infiltration capacity (liters per second log10 transformed) for each site ($F_{11, 109} = 2.52$, P = 0.007). Sites are arranged on the x-axis with development increasing from left to right. Sites that share letters are not significantly different (TukeyHSD).The line in each box represents the median, the box encompasses the 25-75% range of the data, and whiskers show the non-outlier range.

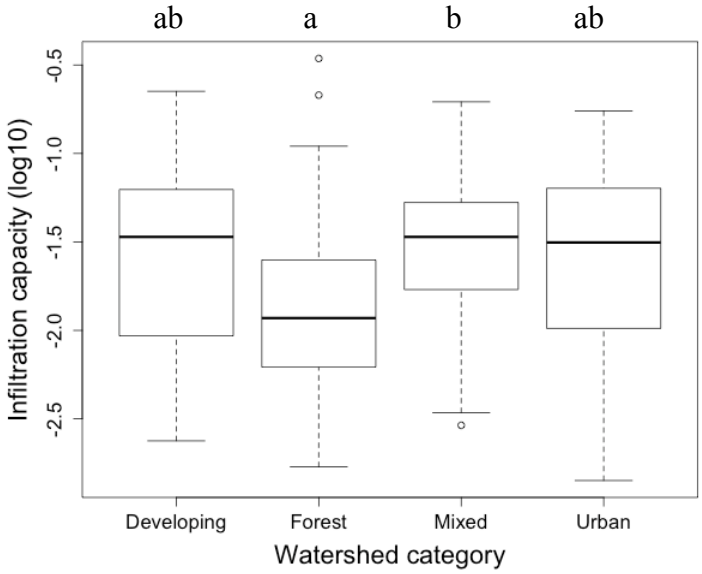


Figure 2-14 Boxplots of soil infiltration capacity (liters per second log10 transformed) grouped by watershed category ($F_{3,117} = 3.11$, $P = 0.03$). Sites that share letters are not significantly different based on a TukeyHSD. The line in each box represents the median, the box encompasses the 25-75% range of the data, and whiskers show the non-outlier range.

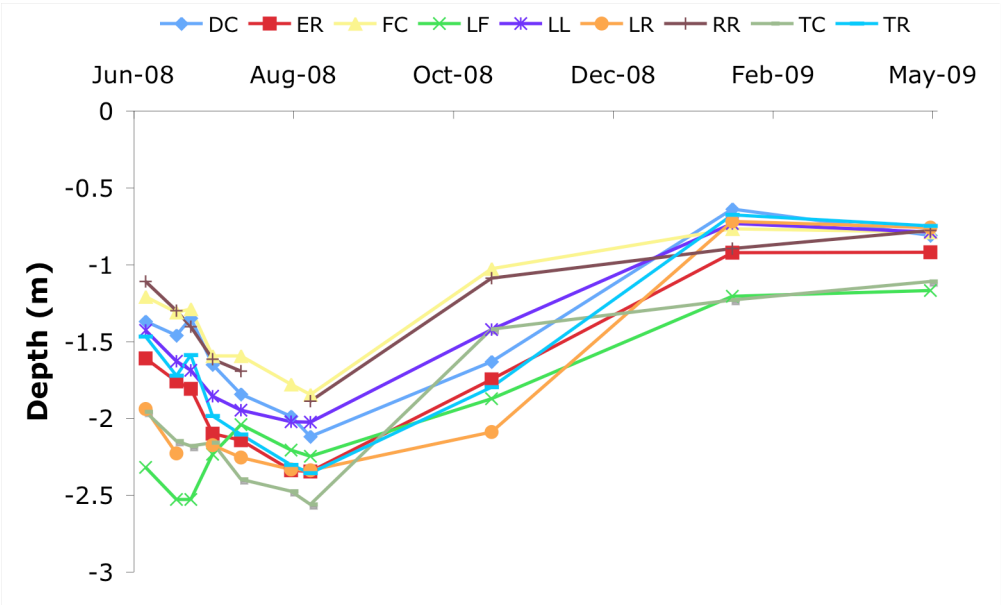


Figure 2-15 Ground water table depths (m, below soil surface) from 6 June 2008 to 1 May 2009 in nine different watersheds ($F_{8,79} = 0.692$, $P = 0.01$). Data are means of 7 wells/site with error bars removed for clarity (see Table 2-1 for site codes).

When I grouped sites by watershed category for analysis I found no significant differences among watershed categories for ground water table depth ($F_{2, 85} = 0.87$, P = 0.42). All sites had similar nutrient availabilities with no significant differences among sites for N, P or K. Not surprisingly, I found no correlations between transplant species' growth and soil nutrient availability (Table. 2-4 & 2-5).

Table 2-4 Results of first season mean maximum growth of all species as a function of soil nutrients.

| | P | | K | | $NO_3$ | |
|---|---|---|---|---|---|---|
| SPECIES | $R^2$ | P | $R^2$ | P | $R^2$ | P |
| AC | 0.18 | 0.25 | 0.31 | 0.12 | 0.00 | 0.93 |
| AN | 0.03 | 0.68 | 0.18 | 0.26 | 0.01 | 0.77 |
| CL | 0.16 | 0.28 | 0.01 | 0.82 | 0.16 | 0.28 |
| P | 0.08 | 0.47 | 0.11 | 0.40 | 0.04 | 0.63 |

Table 2-5 Results of second season mean maximum growth of all species as a function of soil nutrients.

| | P | | K | | $NO_3$ | |
|---|---|---|---|---|---|---|
| SPECIES | $R^2$ | P | $R^2$ | P | $R^2$ | P |
| AC | 0.08 | 0.45 | 0.00 | 0.88 | 0.14 | 0.32 |
| AN | 0.00 | 0.91 | 0.35 | 0.10 | 0.01 | 0.78 |
| CL | 0.03 | 0.68 | 0.04 | 0.61 | 0.07 | 0.50 |
| P | 0.01 | 0.83 | 0.22 | 0.21 | 0.00 | 0.99 |

TRANSPLANT EXPERIMENT

Transplant survival differed among watersheds in the first and second growing season, but there were no consistent patterns among species or watershed categories. Only in the first growing season was an increase in watershed development positively correlated with *A. canadense* survival ($R^2 = 0.51$, P = 0.03) and (Figure 2-16). In the second growing season increased watershed development ($R^2 = 0.44$, P = 0.05) and *C. latifolium* survival were significantly negatively correlated (Figure 2-17). Watershed

development did not affect L. *sinense* survival in either season (Yr 1: $R^2 = 0.33$, P = 0.11; Yr 2: $R^2 = 0.06$, P = 0.54). However, both regressions showed a negative slope indicating a downward trend as development increases.

Within a species there was variation in survival rates among the different sites (Figures 2-18 – 2-21). Results of the GLM indicate that at some sites final survival is significantly higher or lower than the mean. These results did not fit any pattern, revealing that individuals and species reacted differently to local conditions at each site. When I analyzed survival rates using sites grouped in watershed land cover categories I found no significant differences in survival rates of any species in urban, mixed or forested watersheds (Figures 2-22 – 2-25).

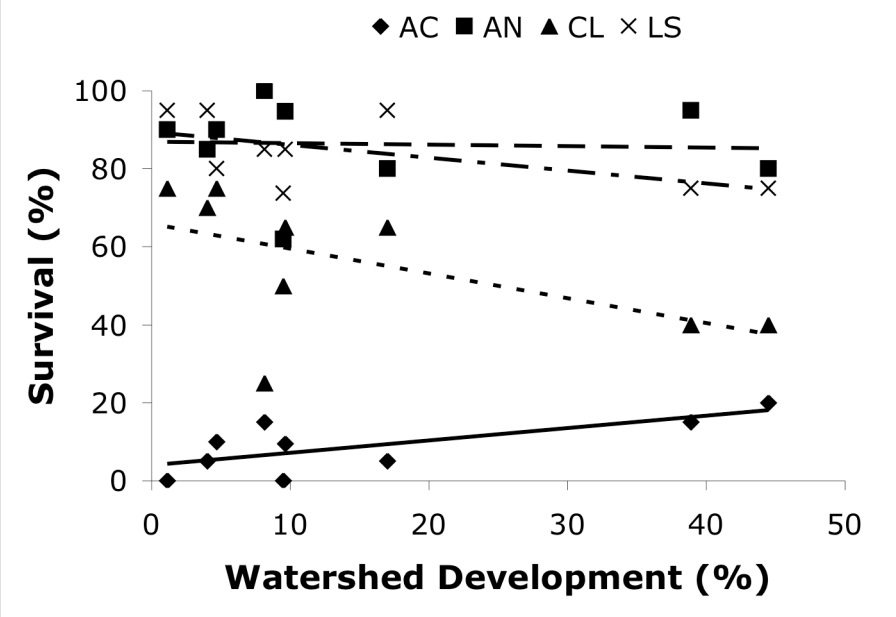


Figure 2-16 First growing season seedling survival (%) of four different species in nine different floodplain forests as a function of watershed development (%). N=20 individuals/species/site. AC – *Allium canadense* ($R^2 = 0.51$, P = 0.03); AN – *Acer negundo* ($R^2 = 0.00$, P = 0.90); CL- *Chasmanthium latifolium* ($R^2 = 0.31$, P = 0.12); LS- *Ligustrum sinense* ($R^2 = 0.33$, P = 0.11)

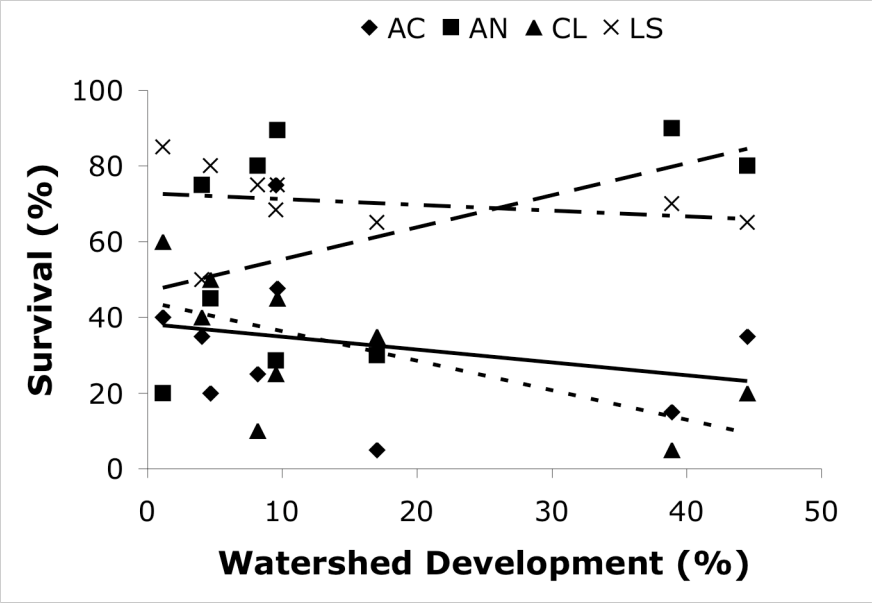


Figure 2-17 Second growing season seedling survival (%) of four different species in nine different floodplain forests as a function of watershed development (%). N=20 individuals/species/site. Second growin AC – *Allium canadense* ($R^2 = 0.07$, P = 0.50); AN – *Acer negundo* ($R^2 = 0.22$, P = 0.21); CL- *Chasmanthium latifolium* ($R^2 = 0.44$, P = 0.05); LS- *Ligustrum sinense*($R^2 = 0.06$, P = 0.54)

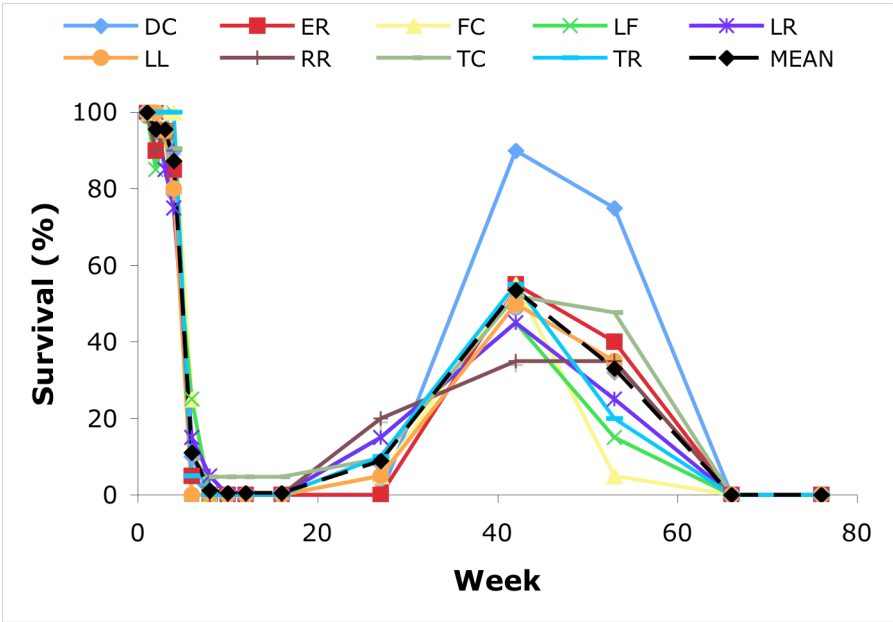


Figure 2-18 *Allium canadense* survival (%) in nine different floodplain forests over a 76 week period. Dashed line represents the mean of all sites. These sites are significantly higher (DC$^{*}$) or lower (FC$^{**}$, LF$^{**}$, LR$^{*}$, TR$^{*}$) than the mean. Asterisks indicate significance based on a binomial GLM of the 53$^{rd}$ week survival rates (*P < 0.05, **P < 0.01, ***P < 0.001).

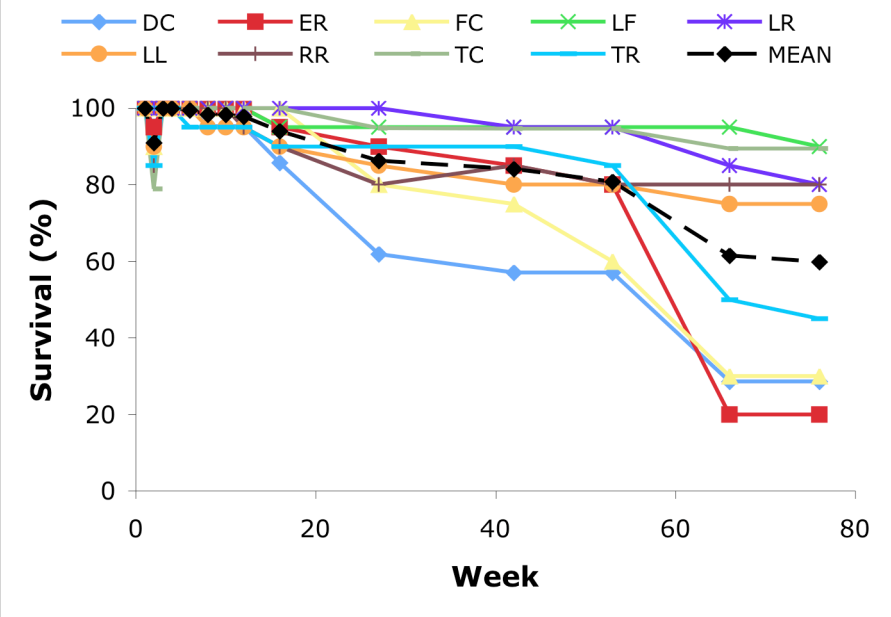


Figure 2-19 *Acer negundo* survival (%) in nine different floodplain forests over a 76 week period. Dashed line represents the mean of all sites. These sites are significantly higher (LF$^{**}$, LR$^{*}$, LL$^{*}$, RR$^{*}$, TC$^{**}$) or lower (ER$^{*}$) than the mean. Asterisks indicate significance based on a binomial GLM of the 76$^{th}$ week survival rates (*P < 0.05, **P < 0.01, ***P < 0.001).

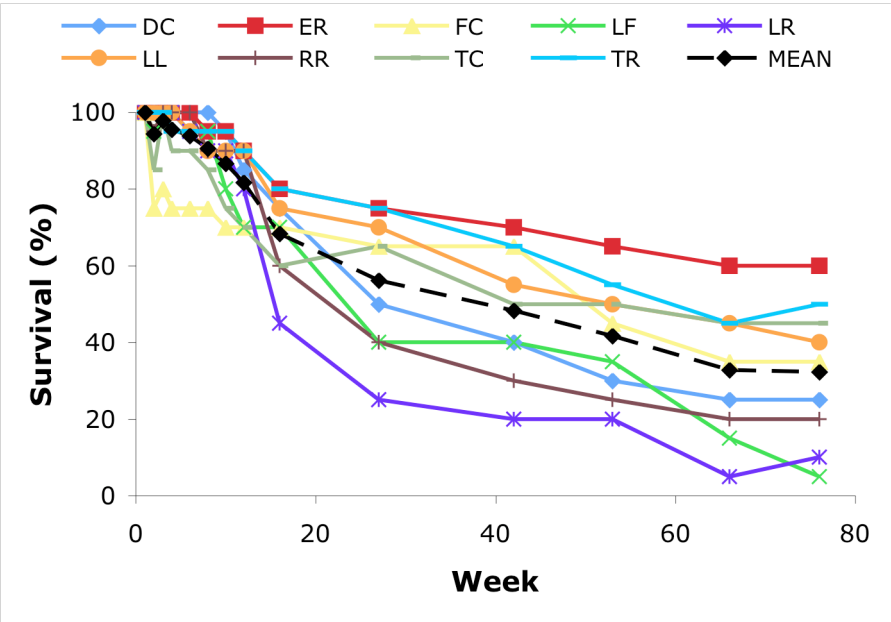


Figure 2-20 *Chasmanthium latifolium* survival (%) in nine different floodplain forests over a 76 week period. Dashed line represents the mean of all sites. These sites are significantly higher or lower (DC$^{*}$, LF$^{**}$, LR$^{**}$, RR$^{*}$) than the mean. Asterisks indicate significance based on a binomial GLM of the 76$^{th}$ week survival rates (*P < 0.05, **P < 0.01, ***P < 0.001).

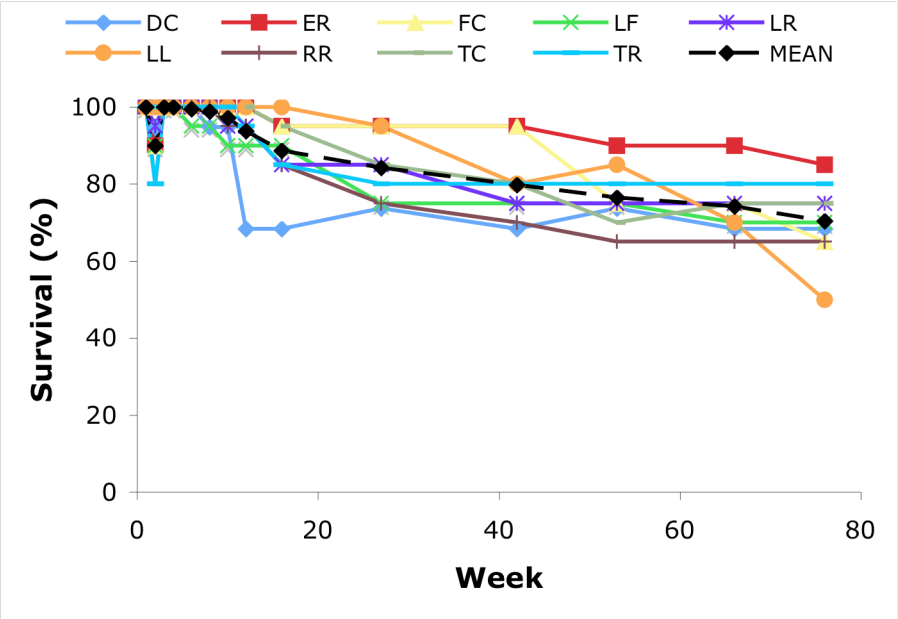


Figure 2-21 *Ligustrum sinense* survival (%) in nine different floodplain forests over a 76 week period. Dashed line represents the mean of all sites. These sites are significantly higher (ER$^{**}$, LR$^{*}$, TC$^{*}$, TR$^{*}$) or lower than the mean. Asterisks indicate significance based on a binomial GLM of the 76$^{th}$ week survival rates (*P < 0.05, **P < 0.01, ***P < 0.001).

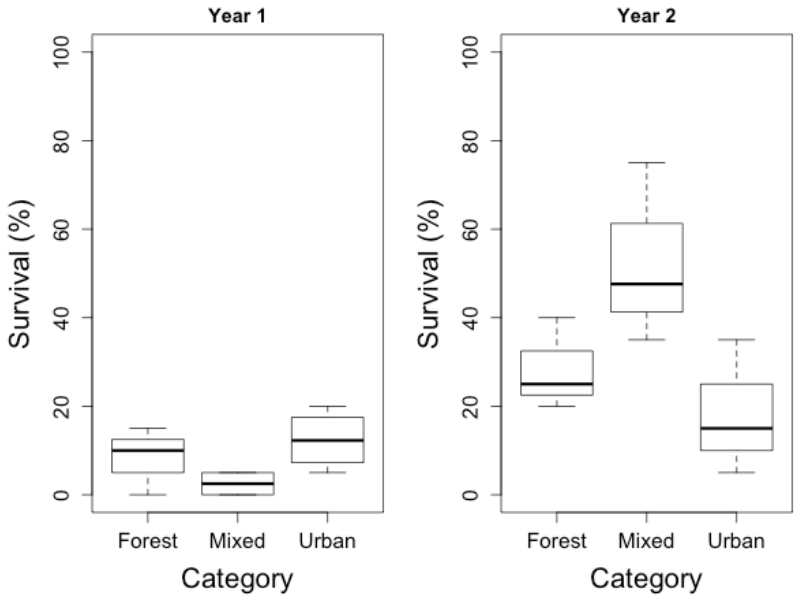


Figure 2-22 Boxplots of *Allium canadense* survival (%) in different watershed categories over two years (Yr 1 $F_{2,6} = 1.53$, P = 0.29; Yr 2 $F_{2,6} = 3.66$, P = 0.09). The line in each box represents the median, the box encompasses the 25-75% range of the data, and whiskers show the non-outlier range.

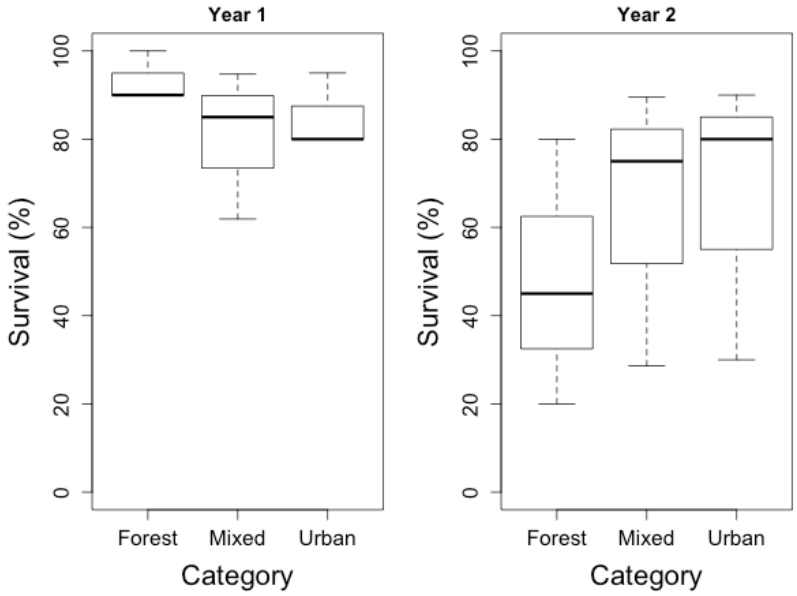


Figure 2-23 Boxplots of *Acer negundo* survival (%) in different watershed categories over two years (Yr 1 $F_{2,6} = 0.97$, P = 0.43; Yr 2 $F_{2,6} = 0.30$, P = 0.75). The line in each box represents the median, the box encompasses the 25-75% range of the data, and whiskers show the non-outlier range.

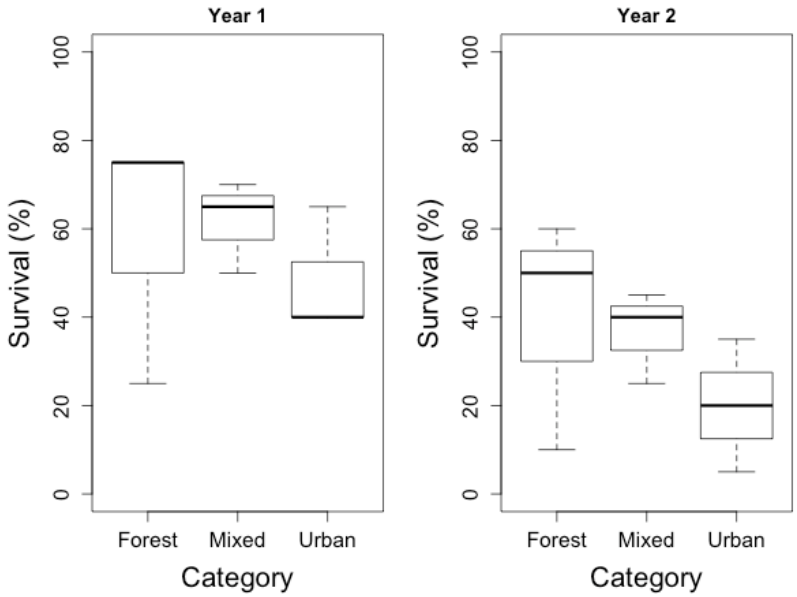


Figure 2-24 Boxplots of *Chasmanthium latifolium* survival (%) in different watershed categories over two years (Yr 1 $F_{2,6} = 0.38$, P = 0.70; Yr 2 $F_{2,6} = 1.0$, P = 0.42). The line in each box represents the median, the box encompasses the 25-75% range of the data, and whiskers show the non-outlier range.

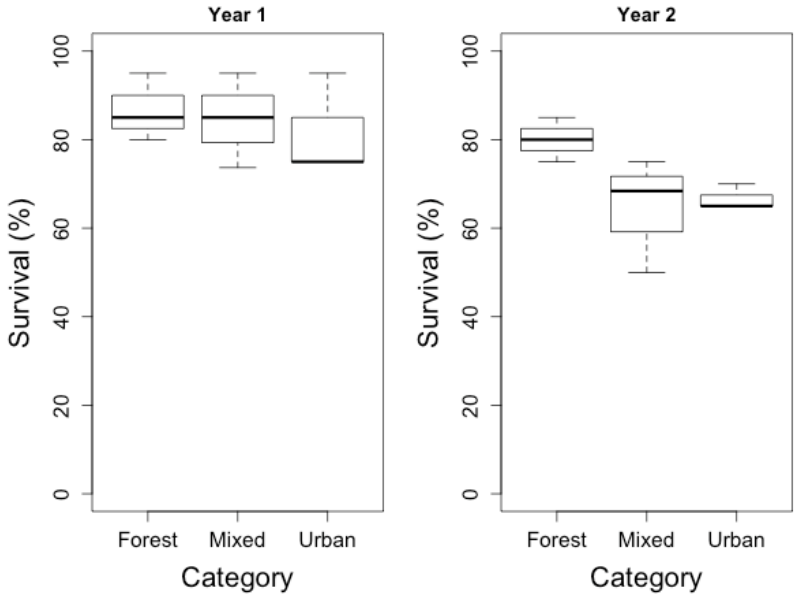


Figure 2-25 Boxplots of *Ligustrum sinense* survival (%) in different watershed categories over two years (Yr 1 $F_{2,6} = 0.19$, P = 0.84; Yr 2 $F_{2,6} = 3.16$ P = 0.12). The line in each box represents the median, the box encompasses the 25-75% range of the data, and whiskers show the non-outlier range.

However, survival rates varied significantly among species and seasons. First season survival rates were significantly different among species ($F_{3,32} = 80.47$, P < 0.0001) and highest for *A. negundo* and *L. sinense*, and lowest for *A. canadense*. (Figure 2-26 Yr 1). Differences in survival rates among species in season two were again significant ($F_{3,32} = 7.91$, P = 0.0004) with *L. sinense* survival remaining very high while *A. negundo* survival dropped somewhat, although differences between the two woody species are not significant (Figure 2-26 Yr 2). However, there is a noticeably larger variation (driven by differences in survival rates among sites) in survival for *A. negundo*. The two herbaceous species *A. canadense* and *C. latifolium* show similar but significantly lower survival compared to the woody species (Figure 2-26 Yr 2). The fact that survival of *A. canadense* is higher in the second growing season than in the first is a function of earlier senescence in season one and thus, some plants counted as dead in season one re-emerged in season two.

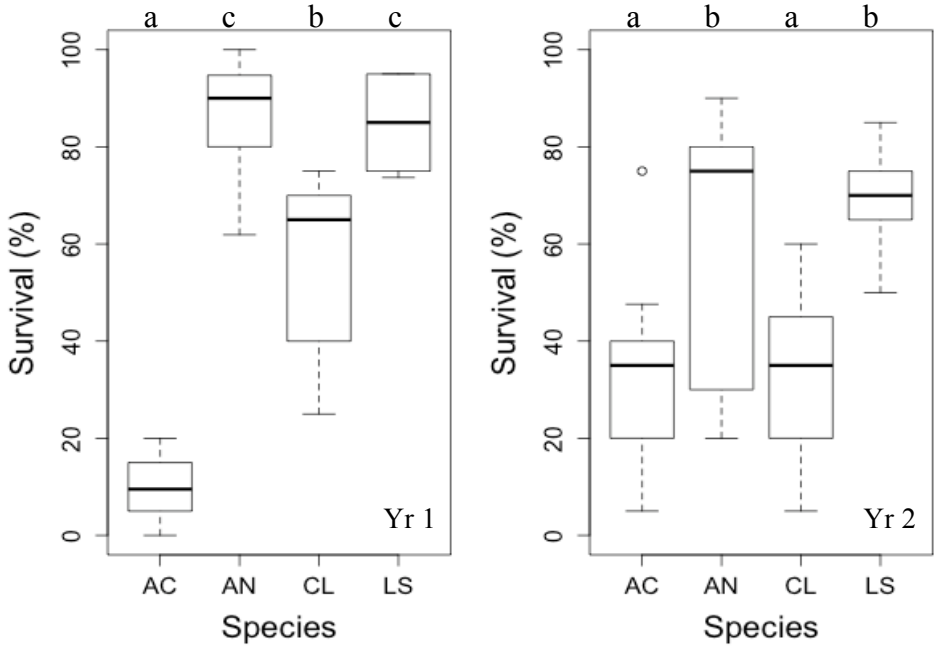


Figure 2-26 Boxplots of species transplant survival (%) from all sites for both growing seasons (Yr 1 $F_{3,32} = 80.47$, $P < 0.0001$; Yr 2 $F_{3,32} = 7.91$, $P = 0.0004$). Species that share letters are not significantly different (TukeyHSD). The line in each box represents the median, the box encompasses the 25-75% range of the data, and whiskers show the non-outlier range.

Contrary to expectations, seedling maximum growth was not correlated to watershed development for any species, including *L. sinense* (Figure 2-27 & 2-28). In general, differences in seedling growth among species were small in season one, but species-specific responses to growing conditions in individual watersheds became more pronounced in the second season. Differences in *A. canadense* growth were not significant in the first ($F_{8,171} = 1.57$, $P = 0.14$), but significant in the second season ($F_{8,91} = 4.29$, $P = 0.0002$) with exceptionally poor seedling growth at the Tyger River and Fairforest Creek sites (Figure 2-29). For *A. negundo* differences in growth among sites were highly significant in both seasons (Yr 1 $F_{8,171} = 10.74$, $P < 0.0001$; Yr 2 $F_{8,144} = 9.22$, $P < 0.0001$) with superior seedling performance at the Tyger River and

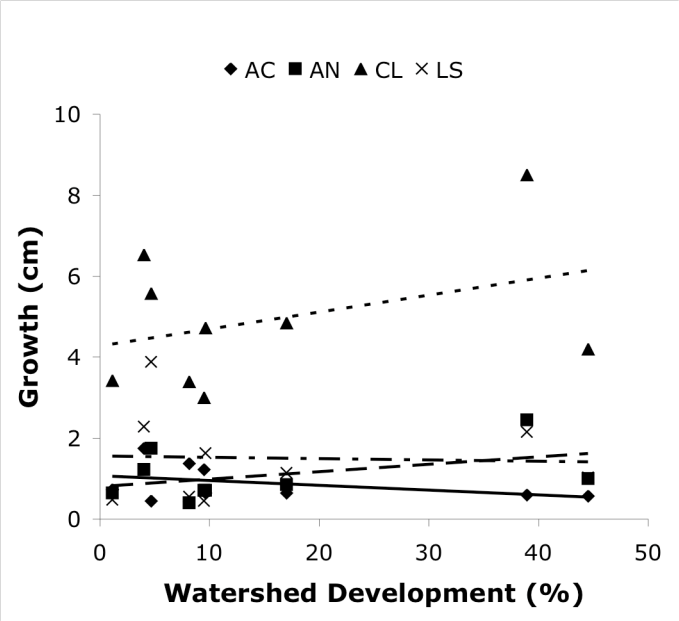


Figure 2-27 First growing season maximum growth (cm) of four different species in nine different floodplain forests as a function of watershed development (%). Data are means from 9 field sites with error bars removed for clarity. AC – *Allium canadense* ($R^2 = 0.15$, P = 0.31); AN – *Acer negundo* ($R^2 = 0.24$, P = 0.18); CL- *Chasmanthium latifolium* ($R^2 = 0.19$, P = 0.24); LS- *Ligustrum sinense* ($R^2 = 0.00$, P = 0.99)

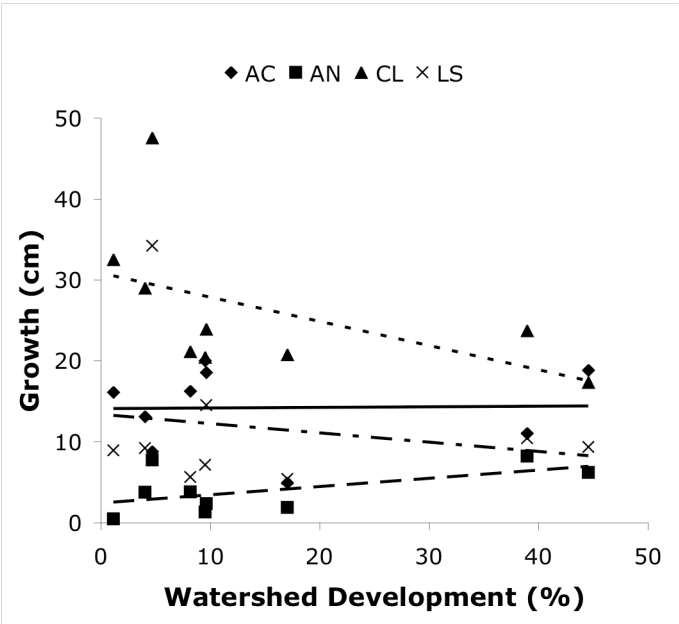


Figure 2-28 Second growing season maximum growth (cm) of four different species in nine different floodplain forests as a function of watershed development (%). Data are means from 9 field sites with error bars removed for clarity. AC – *Allium canadense* ($R^2 = 0.00$, P = 0.91); AN – *Acer negundo* ($R^2 = 0.32$, P = 0.11); CL- *Chasmanthium latifolium* ($R^2 = 0.23$, P = 0.19); LS- *Ligustrum sinense* ($R^2 = 0.04$, P = 0.62)

Lawson's Fork Creek (Figure 2-30). For *C. latifolium* differences in growth among sites were significant in both seasons (Yr 1 $F_{8,171} = 6.16$, $P < 0.0001$; Yr 2 $F_{8,85} = 3.43$, $P = 0.002$) with superior seedling performance at Lawson's Fork in year one and at the Tyger River in year two (Figure 2-31). For *L. sinense* differences in growth among sites were highly significant in both years (Yr 1 $F_{8,171} = 5.99$, $P < 0.0001$; Yr 2 $F_{8,139} = 16.95$, $P < 0.0001$) with seedlings performing best at the Tyger River in both seasons (Figure 2-32). There is no single site offering equally favorable conditions for all species, even a site like the Tyger River, where three of four species perform well, *A canadense* shows the lowest growth. When I analyzed differences in seedling maximum growth by grouping sites into watershed cover categories (forest, mixed, urban), results differed between the first and second growing seasons. I found no effect of watershed categories on seedling growth for any species in the first season, but major differences in the second (Figures 2-33 – 2- 36). But species differed in their responses with maximum growth of *A. negundo* in urban, *C. latifolium* and *L. sinense* in forested, and *A. canadense* in mixed watersheds.

Comparing the two woody transplant species, *A. negundo* and *L. sinense,* I found no significant difference in year one maximum growth ($W = 16823.5$, $P = 0.46$; Figure 2-37) between *A. negundo* cm) and *L. sinense* , but *L. sinense* seedlings outgrew *A. negundo* in the second growing season and these differences in growth were highly significant ($W = 6218$, $P < 0.0001$; Figure 2-37) . I did not compare the growth of the two herbaceous species since they belong to very different functional groups and show different growth forms and phenology.

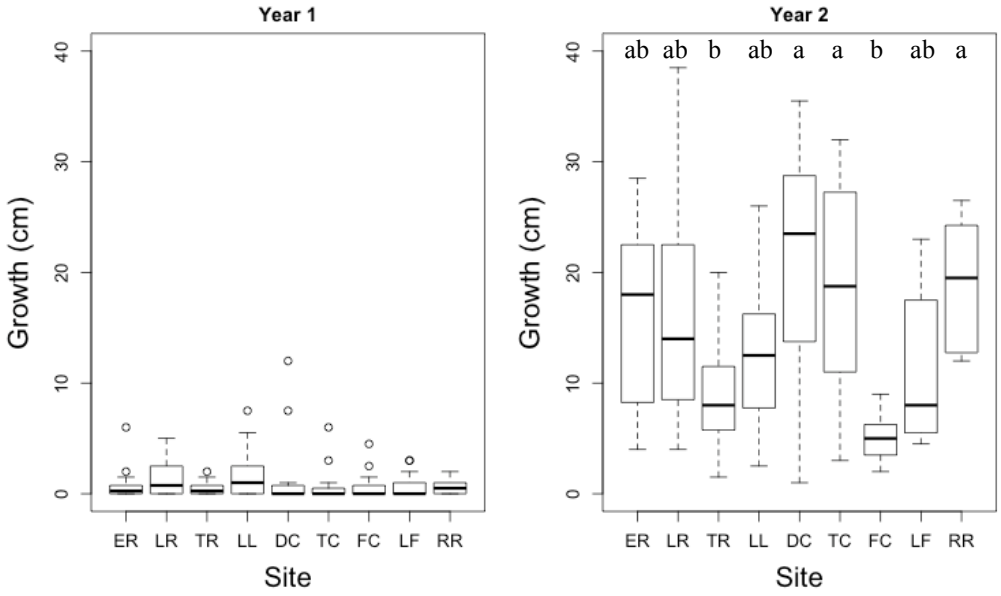


Figure 2-29 Boxplots of maximum growth (cm) of *Allium canadense* for both growing seasons (Yr 1 $F_{8,171} = 1.57$, $P = 0.14$; Yr 2 $F_{8,91} = 4.29$, $P = 0.0002$). Sites are arranged on the x-axis with development increasing from left to right. Sites that share letters are not significantly different based on a TukeyHSD. The line in each box represents the median, the box encompasses the 25-75% range of the data, and whiskers show the non-outlier range.

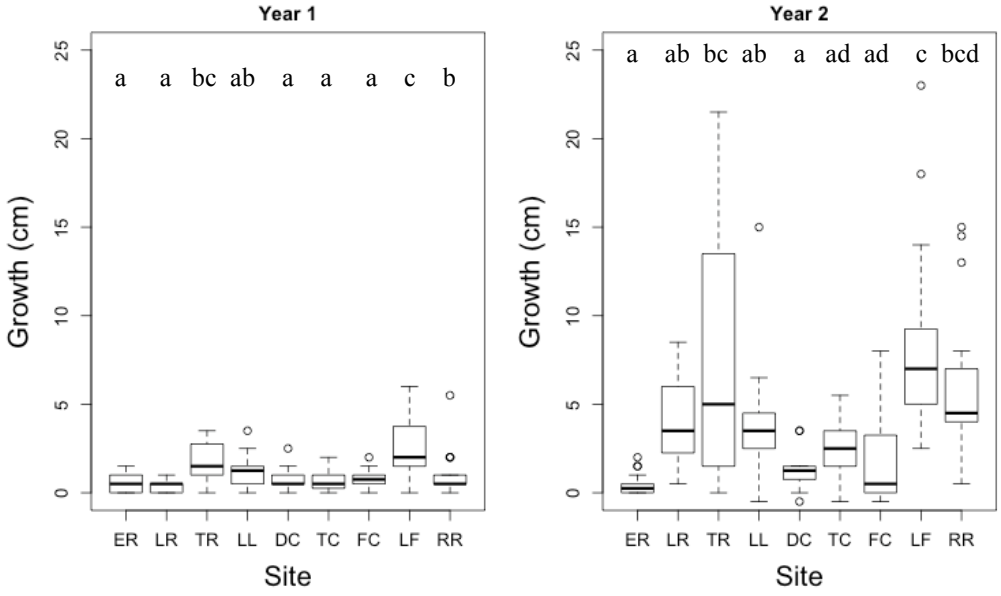


Figure 2-30 Boxplots of maximum growth (cm) of *Acer negundo* for both growing seasons (Yr 1 $F_{8,171} = 10.74$, $P < 0.0001$; Yr 2 $F_{8,144} = 9.22$, $P < 0.0001$). Sites are arranged on the x-axis with development increasing from left to right. Sites that share letters are not significantly different based on a TukeyHSD. The line in each box represents the median, the box encompasses the 25-75% range of the data, and whiskers show the non-outlier range.

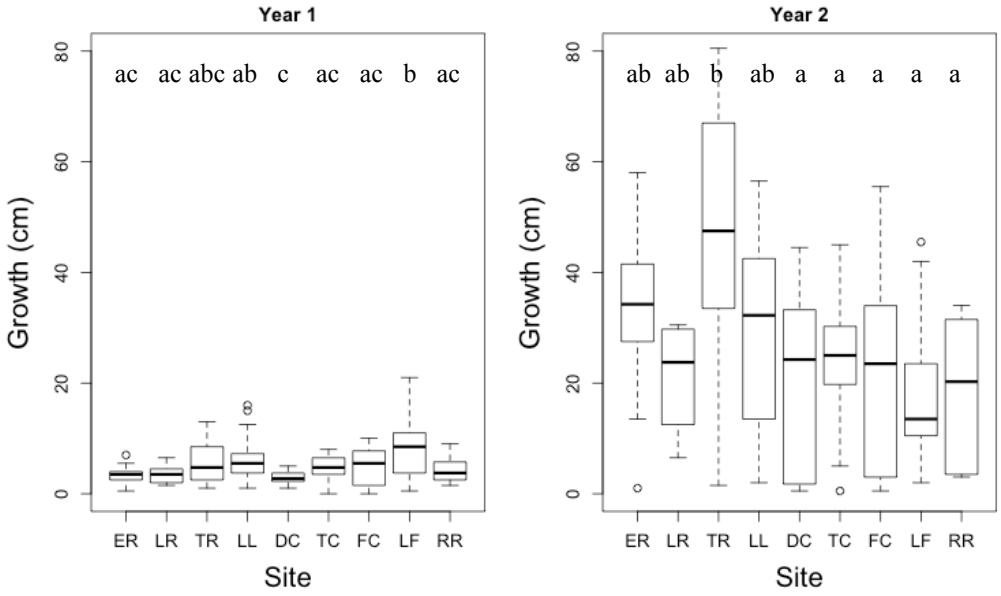


Figure 2-31 Boxplots of maximum growth (cm) of *Chasmanthium latifolium* for both growing seasons (Yr 1 $F_{8,171} = 6.16$, $P < 0.0001$; Yr 2 $F_{8,85} = 3.43$, $P = 0.002$). Sites are arranged on the x-axis with development increasing from left to right. Sites that share letters are not significantly different based on a TukeyHSD. The line in each box represents the median, the box encompasses the 25-75% range of the data, and whiskers show the non-outlier range.

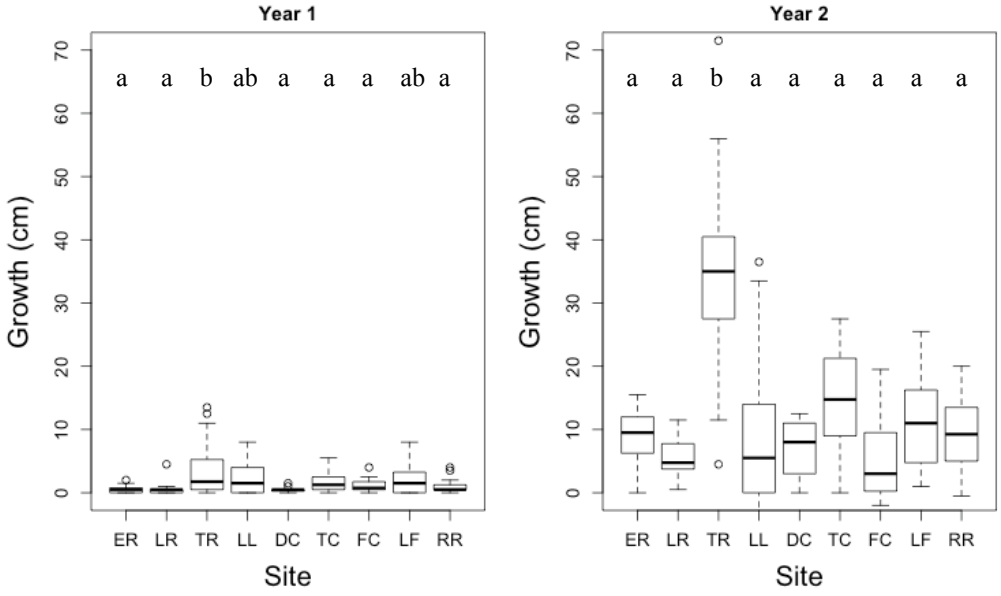


Figure 2-32 Boxplots of maximum growth (cm) of *Ligustrum sinense* for both growing seasons (Yr 1 $F_{8,171} = 5.99$, $P < 0.0001$; Yr 2 $F_{8,139} = 16.95$, $P < 0.0001$). Sites are arranged on the x-axis with development increasing from left to right. Sites that share letters are not significantly different based on a TukeyHSD. The line in each box represents the median, the box encompasses the 25-75% range of the data, and whiskers show the non-outlier range.

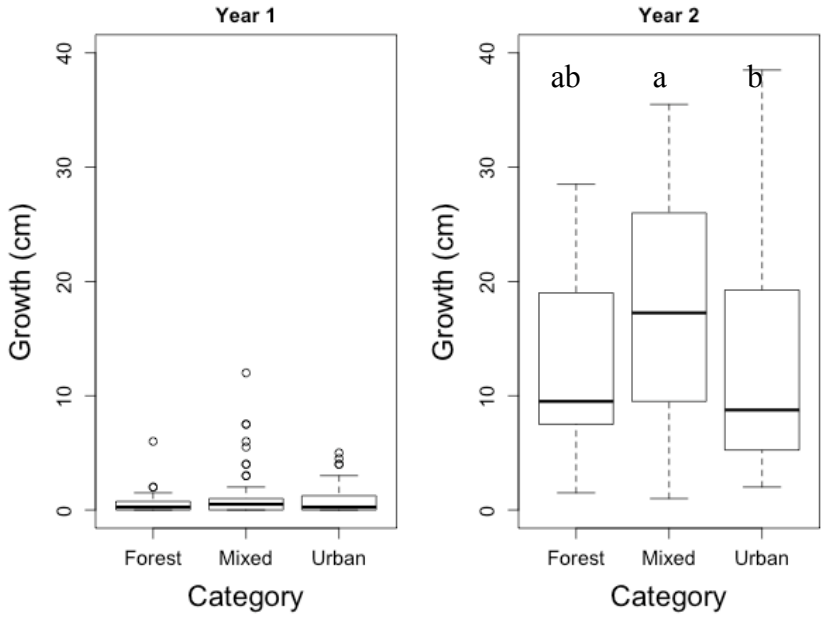


Figure 2-33 Boxplots of maximum growth (cm) of *Allium canadense* by watershed category for both growing seasons (Yr 1 $F_{2,177} = 1.93$, P = 0.15; Yr 2 $F_{2,97} = 4.55$, P = 0.01). Categories that share letters are not significantly different based on a TukeyHSD. The line in each box represents the median, the box encompasses the 25-75% range of the data, and whiskers show the non-outlier range.

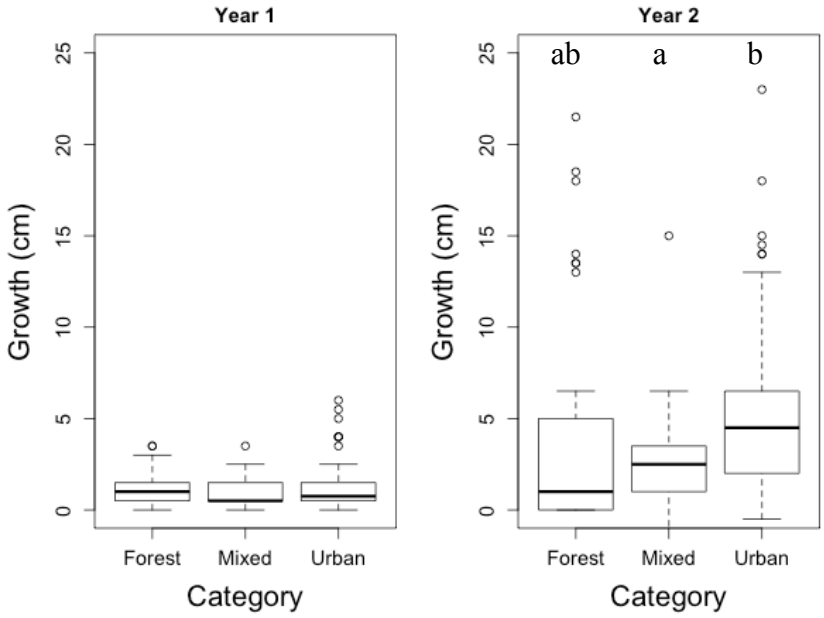


Figure 2-34 Boxplots of maximum growth (cm) of *Acer negundo* by watershed category for both growing seasons (Yr 1 $F_{2,177} = 1.64$, P = 0.20; Yr 2 $F_{2,150} = 4.59$, P = 0.01). Categories that share letters are not significantly different based on a TukeyHSD. The line in each box represents the median, the box encompasses the 25-75% range of the data, and whiskers show the non-outlier range.

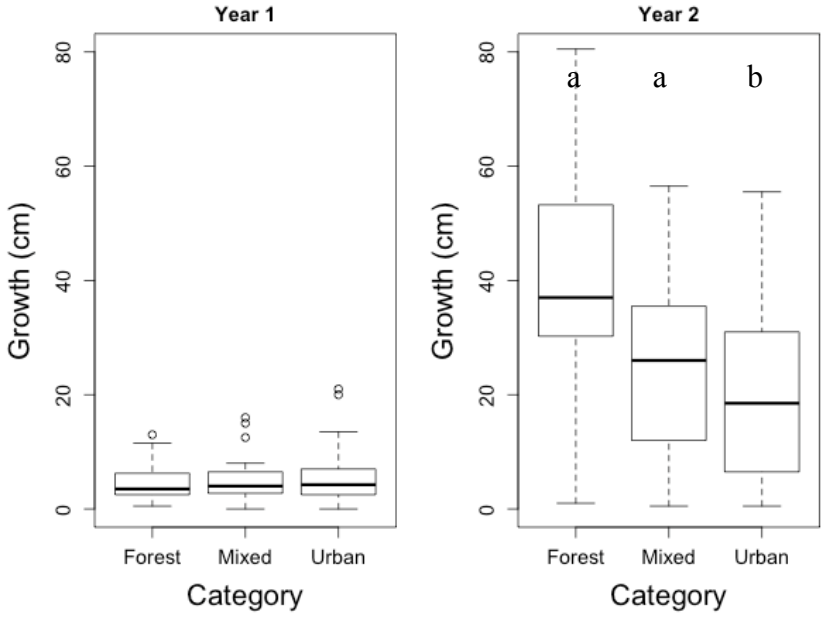


Figure 2-35 Boxplots of maximum growth (cm) of *Chasmanthium latifolium* by watershed category for both growing seasons (Yr 1 $F_{2,177} = 0.68$, $P = 0.51$; Yr 2 $F_{2,91} = 10.51$, $P < 0.0001$). Categories that share letters are not significantly different based on a TukeyHSD. The line in each box represents the median, the box encompasses the 25-75% range of the data, and whiskers show the non-outlier range.

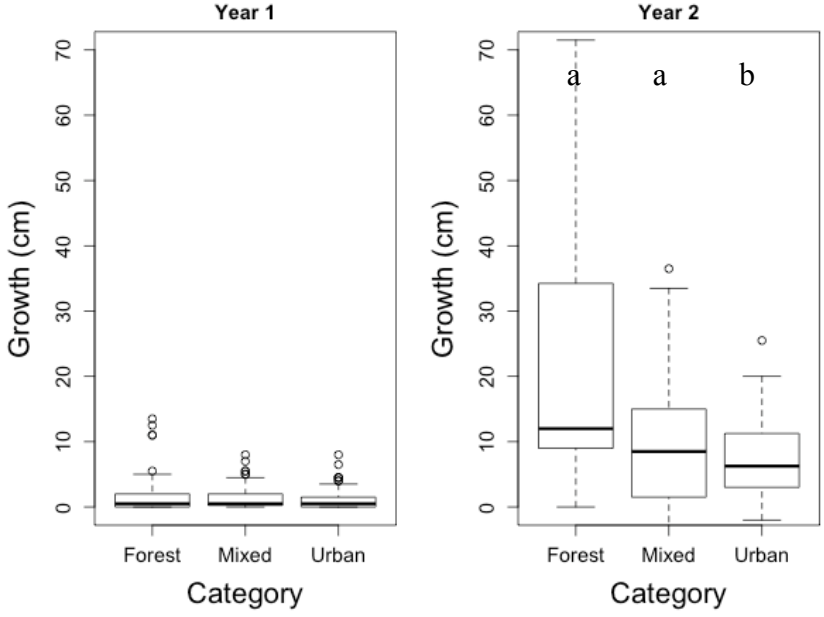


Figure 2-36 Boxplots of maximum growth (cm) of *Ligustrum sinense* by watershed category for both growing seasons (Yr 1 $F_{2,177} = 2.53$, $P = 0.08$; Yr 2 $F_{2,145} = 16.87$, $P < 0.0001$). Categories that share letters are not significantly different based on a TukeyHSD. The line in each box represents the median, the box encompasses the 25-75% range of the data, and whiskers show the non-outlier range.

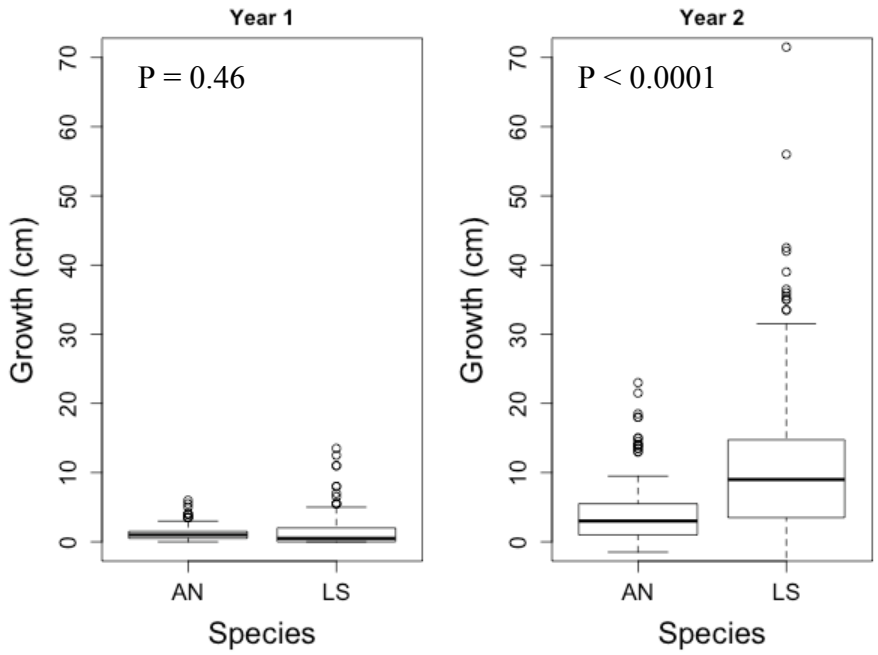


Figure 2-37 Boxplots of maximum growth (cm) of all living individuals of *Acer negundo* (AN) and *Ligustrum sinense* (LS) for both growing seasons. The line in each box represents the median, the box encompasses the 25-75% range of the data, and whiskers show the non-outlier range.

When I compared relative growth rates (RGR, cm/day) of surviving *A. negundo* and *L. sinense* over two growing seasons, results of the linear mixed effects model show differences in second growing season (Figure 2-38), but none were lower than the conservative initial Holm – Bonferroni correction of P = 0.004 (Table 2-6). RGR of *L. sinense* was higher than *A.negundo* seven out of the thirteen sampling periods and from the twelfth week on was always higher except for the winter measurement. RGR was highest in the early spring for both *A. negundo* (0.34 ± 0.09 mm/day) and *L. sinense* (0.82 ± 0.11 mm/day).

I found large differences in herbivore attack rates among species and these differences were significant for all sampling periods with *L. sinense* consistently showing the lowest herbivory (Table 2-7). After the 42$^{nd}$ week, the vast majority of *A. negundo* and

*C. latifolium* seedlings had visual signs of herbivory while fewer *L. sinense* individuals were attacked (Figure 2-39)..

**Discussion**

I conducted landscape and local analyses of factors shaping invasion success of *L. sinense* in South Carolina floodplain forests. My results confirm previously reported associations of *L. sinense* with increased urbanization(Loewenstein & Loewenstein 2005; Burton & Samuelson 2008), a pattern reported for many other invasive species (McKinney 2002). However, contrary to my expectations, landscape level disturbances (watershed development, amount of impervious surfaces) or lack thereof (forest cover and distance to urban areas) do not provide mechanisms explaining the differences in performance of *L. sinense* or of the native species it replaces. Urbanization is reported to cause increased sediment loads (Trimble 1997), stream

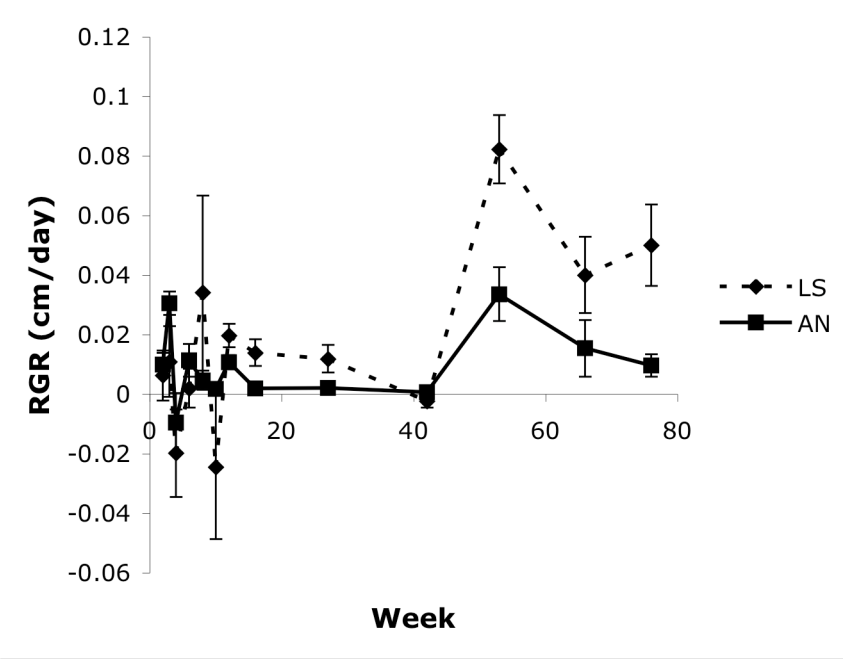


Figure 2-38 Relative growth rates (RGR, cm/day) of *Acer negundo* (AN) and *Ligustrum sinense* (LS) over a 76 week period. Data are means (± 1SE) from nine field sites of up to 20 individuals/species/site.

Table 2-6 Results of a linear mixed effects model comparing relative growth rates (RGR, cm/day) as a fixed effect of species (*Acer negundo* and *Ligustrum sinense*) with site (nine sites) as a random effect over a 76 week period. Values that are bold are significant based on a Holm – Bonferroni correction for multiple comparisons.

| Week | Species | Value | SE | t - value | p - value |
|---|---|---|---|---|---|
| 2 | AN | 0.010 | 0.007 | 1.52 | 0.170 |
| 2 | LS | -0.004 | 0.009 | -0.39 | 0.700 |
| 3 | AN | 0.031 | 0.009 | 3.46 | 0.009 |
| 3 | LS | -0.020 | 0.012 | -1.59 | 0.150 |
| 4 | AN | -0.010 | 0.013 | -0.76 | 0.470 |
| 4 | LS | -0.010 | 0.017 | 0.61 | 0.560 |
| 6 | AN | 0.011 | 0.006 | 1.88 | 0.100 |
| 6 | LS | -0.009 | 0.005 | -2.01 | 0.080 |
| 8 | AN | 0.005 | 0.023 | 0.20 | 0.850 |
| 8 | LS | 0.029 | 0.033 | 0.90 | 0.390 |
| 10 | AN | 0.002 | 0.017 | 0.11 | 0.910 |
| 10 | LS | -0.026 | 0.024 | -1.09 | 0.310 |
| 12 | AN | 0.011 | 0.003 | 3.27 | 0.010 |
| 12 | LS | 0.009 | 0.004 | 2.08 | 0.070 |
| 16 | AN | 0.002 | 0.003 | 0.57 | 0.580 |
| 16 | LS | 0.012 | 0.005 | 2.58 | 0.030 |
| 27 | AN | 0.002 | 0.003 | 0.60 | 0.570 |
| 27 | LS | 0.010 | 0.005 | 2.05 | 0.080 |
| 42 | AN | 0.001 | 0.002 | 0.43 | 0.680 |
| 42 | LS | -0.003 | 0.002 | -1.47 | 0.180 |
| 53 | AN | 0.034 | 0.010 | 3.25 | 0.010 |
| 53 | LS | 0.049 | 0.010 | 3.46 | 0.009 |
| 66 | AN | 0.015 | 0.010 | 1.37 | 0.210 |
| 66 | LS | 0.025 | 0.007 | 3.52 | 0.008 |
| 76 | AN | 0.010 | 0.010 | 0.95 | 0.370 |
| 76 | LS | 0.040 | 0.010 | 3.45 | 0.009 |

incision and lowered near-stream ground water table (Groffman et al. 2003), and alterations in natural flow regimes (Poff et al. 1997; Walsh et al. 2005; Schoonover, Lockaby, & Helms 2006). However, although I documented strong gradients in land cover types (Table 2-3), I found only small differences in the abiotic properties of the floodplain forests between developed or forested watershed. My observations of sites and soil types did not reveal any obvious differences and I found no differences in soil infiltration capacity (Figure 2-13) and ground water table depths among sites (Figure 2-15).

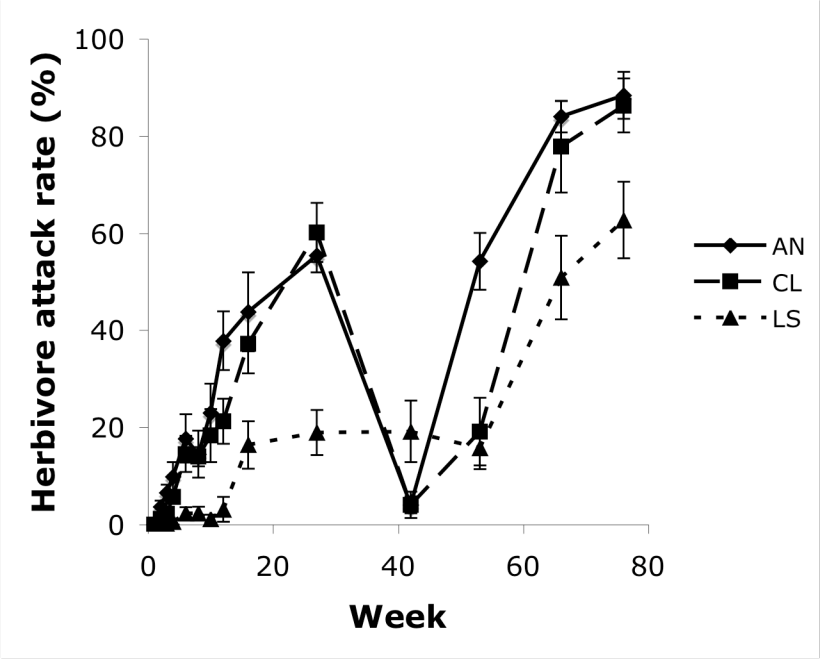


Figure 2-39 –Herbivore attack rates (%) on transplanted seedlings of *Acer negundo* (AN), *Chasmanthium latifolium* (CL), and *Ligustrum sinense* (LS) over a 76-week period. Data are means (±1SE) of attack rates in nine different floodplain forests (average of up to 20 individuals/species/site).

While I cannot rule out effects of past habitat modification (Walter and Merritts 2008), or climate change induced drought (Zhang et al. 2007), it appears that current increased urbanization in my study area does not result in significant alterations in abiotic conditions in the watersheds. Consequently, watershed development (and the assumed resulting alterations in abiotic conditions) is not the mechanism promoting *L. sinense* invasion and disappearance of the native vegetation.

While I did not directly manipulate disturbance regimes, I expected differences in watershed land cover in my selected watersheds to cause differences in survival or growth favoring *L. sinense* in developed watersheds. Flooding disturbance in riparian habitats increase exotic species (Brown and Peet 2003) and other invasive shrubs such as *Tamarix* have been shown to respond to hydrology driven disturbance alterations (Stromberg et al. 2007). This would provide a mechanism to explain the existing distribution and abundance pattern (Figures 2-3– 2-6) I documented in the various

Table 2-7 Results of a linear mixed effects model comparing herbivore attack rates (%) as a fixed effect of species (*Acer negundo*, *Chasmanthium latifolium*, and *Ligustrum sinense*) with site (nine sites) as a random effect over a 76 week period. Values that are bold are significant based on a Holm – Bonferroni correction for multiple comparisons.

| Week | Species | Value | SE | t - value | p - value |
|---|---|---|---|---|---|
| 2 | AN | 3.65 | 0.91 | 3.99 | **0.0011** |
| 2 | CL | -2.51 | 1.29 | -1.94 | 0.071 |
| 2 | LS | -3.03 | 1.29 | -2.34 | **0.032** |
| 3 | AN | 6.62 | 1.06 | 6.23 | **0.00** |
| 3 | CL | -4.39 | 1.50 | -2.93 | **0.01** |
| 3 | LS | -6.62 | 1.50 | -4.41 | **0.0004** |
| 4 | AN | 9.84 | 1.93 | 5.11 | **0.001** |
| 4 | CL | -4.13 | 2.49 | -1.66 | 0.12 |
| 4 | LS | -9.26 | 2.49 | -3.71 | **0.0019** |
| 6 | AN | 17.74 | 3.65 | 4.86 | **0.0002** |
| 6 | CL | -3.18 | 4.67 | -0.68 | 0.51 |
| 6 | LS | -15.46 | 4.67 | -3.31 | **0.0044** |
| 8 | AN | 14.50 | 3.09 | 4.69 | **0.0002** |
| 8 | CL | -0.52 | 4.00 | -0.13 | 0.90 |
| 8 | LS | -12.16 | 4.00 | -3.04 | **0.0078** |
| 10 | AN | 23.04 | 4.68 | 4.92 | **0.0002** |
| 10 | CL | -4.71 | 6.48 | -0.73 | 0.48 |
| 10 | LS | -21.84 | 6.48 | -3.37 | **0.0039** |
| 12 | AN | 37.84 | 4.64 | 8.15 | **0.00** |
| 12 | CL | -16.56 | 5.74 | -2.88 | **0.011** |
| 12 | LS | -34.72 | 5.74 | -6.04 | **0.00** |
| 16 | AN | 43.80 | 6.54 | 6.70 | **0.00** |
| 16 | CL | -6.55 | 9.25 | -0.71 | 0.49 |
| 16 | LS | -27.4 | 9.25 | -2.96 | **0.0092** |
| 27 | AN | 55.44 | 4.88 | 11.36 | **0.00** |
| 27 | CL | 4.68 | 6.59 | 0.71 | 0.49 |
| 27 | LS | -36.5 | 6.59 | -5.54 | **0.00** |
| 42 | AN | 4.08 | 4.09 | 1.00 | 0.33 |
| 42 | CL | 0.00 | 5.33 | 0.00 | 1.00 |
| 42 | LS | 15.10 | 5.33 | 2.83 | **0.012** |
| 53 | AN | 54.23 | 5.81 | 9.34 | **0.00** |
| 53 | CL | -35.09 | 7.69 | -4.56 | **0.0003** |
| 53 | LS | -38.5 | 7.69 | -5.01 | **0.0001** |
| 66 | AN | 84.00 | 7.61 | 11.04 | **0.00** |
| 66 | CL | -6.19 | 10.76 | -0.58 | 0.57 |
| 66 | LS | -33.16 | 10.76 | -3.08 | **0.0071** |
| 76 | AN | 88.42 | 6.22 | 14.21 | **0.00** |
| 76 | CL | -2.10 | 8.32 | -0.25 | 0.80 |
| 76 | LS | -25.72 | 8.32 | -3.09 | **0.007** |

watersheds. The data from my field sites confirm the lack of differences among watersheds for abiotic variables and contrary to my expectations the explanatory power of watershed development for growth and survival of *L. sinense* were extremely low. This indicates that developed watersheds do not have conditions (abiotic or biotic) to promote *L. sinense* invasion. Moreover, forested watersheds do not appear resistant to *L. sinense* advancement since the species is equally abundant regardless of forest age (indicated by mean native tree DBH), a finding similar to work on other non-native shrub species (Flory and Clay 2009). Survival of *L. sinense* transplants showed little variation among watersheds and ranged from 85 to 50% and I found little differences in growth. My results support the notion that *L. sinense* is a strong invader of floodplain forests and all Piedmont floodplain forests are at risk of invasion. None of the sites I investigated appear to have inherent biotic or abiotic resistance that may reduce *L. sinense* survival or growth.

My transplant experiment using *L. sinense* and three native species provided further insights into local versus watershed factors that may drive abundance of the invader and the native flora. I expected native species to be negatively affected by development, yet the only significant correlation of development was positive for *A. canadense* in the first growing season (Figure 2-16). Overall, growth and survival varied by species and among watersheds, but there was no consistent pattern on a landscape level or for watershed categories. Native seedlings in forested watersheds did not perform any better than seedlings in mixed or developed watersheds. Survival of *L. sinense* seedlings was significantly higher than for *A. canadense* and *C. latifolium*, but this is more reflective of differences in life form (woody shrub vs. herbaceous forb and grass). A better comparison is with the functionally similar *A. negundo*, still *L. sinense* had higher mean survival and the least variation among sites and if the experiment had continued longer these small but accumulating differences

in survival and growth rates should increase *L. sinense*'s competitive edge over native woody species. This performance advantage is further enhanced through an apparent release from predators. I found significantly reduced herbivory on *L. sinense* compared to native *A. negundo* and *C. latifolium* (Figure 2-39) which promotes invasiveness in other invasive species (Carpenter and Cappuccino 2005). The final outcome of the interaction of site conditions with native species and *L. sinense* are heavily invaded floodplain forests where a dense mid level canopy prevents recruitment of native species (Greene, Chp 1) despite apparently suitable growing conditions.

If *L. sinense* is competitively dominant over native species and able to survive and grow equally well in all watersheds, why is *L. sinense* cover strongly correlated with development? Traditional explanations have focused on disturbance induced by urbanization, but my results show little differences in a variety of measures between developed and forested watersheds. This requires consideration of other factors associated with development that may promote invasive species. Propagule pressure is considered an important factor promoting spread and abundance of invasive species (Levine 2001; Von Holle & Simberloff 2005; Lockwood, Cassey, & Blackburn 2005; Eschtruth & Battles 2009). As a horticultural introduction, it is likely that large *L. sinense* populations in developed watersheds and large urban areas are sources of initial introductions into riparian areas. Similar entryways for propagules of invasive species from gardens in urbanized areas into the surrounding landscape matrix are reported for other species (Hutchinson & Vankat 1997; Bartuszevige, Gorchov, & Raab 2006; McDonald & Urban 2006). Once the first propagules arrive and establish, it appears only a question of time before *L. sinense* is able to become competitively dominant and able to transform riparian habitats.

Results from my forest stand surveys show that size class is a significant predictor for both cover and abundance of *L. sinense* (Figures 2-7 – 2-12). Moreover, size of the single largest *L. sinense* individual has a much higher explanatory value than any landscape metric in predicting *L. sinense* prevalence. Since my seedling growth indicated that survival and growth of *L. sinense* are generally similar at all sites, I assume that the largest individuals are also the oldest. Increased *L. sinense* abundance and cover are not the result of more favorable conditions, but are a result of invasion history, making time since first arrival the most important factor for explaining *L. sinense* invasion success. The association of *L. sinense* and human development is likely the result of higher propagule pressure close to human settlements and time since invasion, not disturbance and alterations of abiotic conditions in floodplain forests. Sites with high abundance or cover of *L. sinense* outside of developed watersheds are likely the result of chance long distance dispersal events.

My results have important implications for management of invasive species. While urbanization creates the sources (through ornamental plantings) of propagules that can invade riparian areas in my study region, urbanization does not benefit *L. sinense* or handicap native species by changing abiotic conditions or hydrology. In my particular example, *L. sinense* appears to be the "driver" and not a "passenger" in transformations of Piedmont floodplain forests. Disturbance of the landscape matrix through urbanization appears to be secondary to species traits and propagule pressure of *L. sinense* in explaining distribution patterns. By looking into the past, it gives a clear view of the future. At sites were *L. sinense* has been present for long periods of time *L. sinense* is able to become highly abundant and dense. Increased *L. sinense* cover leads to reduced native plant growth and survival (Osland, Pahl & Richardson 2009; Greene Chp. 1), even in the absence of further urbanization. Even though *L. sinense* is currently most dominant in developed watersheds, more distant and forested

watersheds are not resistant to *L. sinense* invasion. There are no "safe sites" for native plant species. Direct habitat destruction and *L. sinense* are the greatest threats to the long-term sustainability of Piedmont floodplain forests. Assumptions that *L. sinense* has invaded all suitable habitats are premature. Land managers and property owners need to be aware of this ongoing invasion and need to focus their attention on newly invaded areas. Natural processes are not controlling sites with current lower abundance and cover of *L. sinense*, but are likely newer invasions beginning to establish. These incipient invasions should be the focal points for removal because elimination of *L. sinense* effectively resets the invasion trajectory and prevents negative effects of *L. sinense* on native species. But neither of these steps will ultimately be successful without addressing the root cause of *L. sinense* invasion, i.e. the sources of propagules.

Studies like this and others (Predick & Turner 2008; Chytry et al. 2008; Eschtruth & Battles 2009; Flory & Clay 2009) that simultaneously examine local dynamics and landscape level factors promoting invasive species provide critical insights into the mechanisms promoting invasive species. Using a landscape level approach to invasive species (With 2002) results in identifying the key relationships of invasive species distributions. My study also offers a more positive outlook for management of floodplain forests, even if *L. sinense* cannot be completely controlled or eradicated. Urbanization, despite creating habitat loss and many other associated changes, did not have devastating effects on downstream conditions for native plants. While my results also show the importance of local conditions for survival and growth of native species, all watersheds would allow native species to establish. I assume that the absence or low abundance of native species in some of these watersheds is a result of lack of propagule sources that could replenish local populations in areas where *L. sinense* has not yet invaded (or has been controlled). Active restoration through establishment

(planting or seeding) of source populations in upper reaches of my watersheds could allow native species to recolonize downstream floodplain forests. Managers should promote both the establishment of native vegetation as they are trying to prevent initial establishment of *L. sinense*. The assumption that urbanization has changed conditions so that native plants are unable to survive in developed watersheds may have prevented such efforts, but my results clearly show that they are warranted and can be successful.

REFERENCES

Brown, C.E. & Pezeshki, S.R. (2000) Study on waterlogging as a potential tool to control *Ligustrum sinense* populations in Western Tennessee. *Wetlands*, **20**, 429–437.

Brown, D.G., Johnson, K.M., Loveland, T.R. & Theobald, D.M. (2005) Rural land-use trends in the conterminous United States, 1950-2000. *Ecological Applications*, **15**, 1851-1863.

Brown, J.H. & Sax, D.F. (2004) An essay on some topics concerning invasive species. *Austral Ecology*, **29**, 530–536.

Brown, R.L. & Peet, R.K. (2003) Diversity and Invasibility of southern Appalachian Plant Communities. *Ecology*, **84**, 32 – 39.

Burton, M. & Samuelson, L. (2008) Influence of urbanization on riparian forest diversity and structure in the Georgia Piedmont, US. *Plant Ecology*, **195**, 99–115.

Burton, M.L., Samuelson, L.J. & Pan, S. (2005) Riparian woody plant diversity and forest structure along an urban-rural gradient. *Urban Ecosystems*, **8**, 93–106.

Cadenasso, M.L. & Pickett, S.T.A. (2001) Effect of edge structure on the flux of species into forest interiors. *Conservation Biology*, **15**, 91–97.

Carpenter, D. & Cappuccino, N. (2005) Herbivory, time since introduction and the invasiveness of exotic plants. *Journal of Ecology*, **93**, 315–321.

Chytry, M., Jarosik, V., Pysek, P., Hajek, O., Knollova, I., Tichy, L. & Danihelka, J. (2008) Separating habitat invasibility by alien plants from the actual level of invasion. *Ecology*, **89**, 1541–1553.

Cincotta, R.P., Wisnewski, J. & Engelman, R. (2000) Human population in the biodiversity hotspots. *Nature*, **404**, 990–992.

Coates, A.M. (1965) *Garden shrubs and their histories*. E.P. Dutton, New York, NY USA.

Cowell, C.M. (1993) Environmental gradients in secondary forests of the Georgia Piedmont, U.S.A. *Journal of Biogeography*, **20**, 199 – 207.

Crawley, M.J. (1989) The successes and failures of weed biocontrol using insects. *Biocontrol News and Information*, **10**, 213–223.

Didham, R.K., Tylianakis, J.M., Hutchison, M.A., Ewers, R.M. & Gemmell, N.J. (2005) Are invasive species the drivers of ecological change? *Trends in Ecology & Evolution*, **20**, 470–474.

Dukes, J.S. (2001) Biodiversity and invasibility in grassland microcosms. *Oecologia*, **126**, 563–568.

Dukes, J.S. & Mooney, H.A. (1999) Does global change increase the success of biological invaders? *Trends in Ecology & Evolution*, **14**, 135 – 139.

Eschtruth, A.K. & Battles, J.J. (2009) Assessing the relative importance of disturbance, herbivory, diversity, and propagule pressure in exotic plant invasion. *Ecological Monographs*, **79**, 265–280.

Faulkner, S. (2004) Urbanization impacts on the structure and function of forested wetlands. *Urban Ecosystems*, **7**, 89–106.

Flory, S.L. & Clay, K. (2009) Invasive plant removal method determines native plant community responses. *Journal of Applied Ecology*, **46**, 434–442.

Grimm, N.B., Faeth, S.H., Golubiewski, N.E., Redman, C.L., Wu, J., Bai, X. & Briggs, J.M. (2008) Global change and the ecology of cities. *Science*, **319**, 756–760.

Grimm, N.B., Foster, D., Groffman, P., Grove, J.M., Hopkinson, C.S., Nadelhoffer, K.J., Pataki, D.E. & Peters, D.P. (2008) The changing landscape: ecosystem responses to urbanization and pollution across climatic and societal gradients. *Frontiers in Ecology and the Environment*, **6**, 264–272.

Groffman, P.M., Bain, D.J., Brand, L.E., Belt, K.T., Brush, G.S., Grove, J.M., Pouyat, R.V., Yesilonis, I.C. & Zipperer, W.C. (2003) Down by the riverside: urban riparian ecology. *Frontiers in Ecology and the Environment*, **1**, 315–321.

Homer, C., Huang, C., Yang, L., Wylie, B. & Coan, M. (2004) Development of a 2001 National Landcover Database for the United States. *Photogrammetric Engineering and Remote Sensing*, **70**, 829 - 840.

Hook, D., Jr, W.M., Williams, T., Jones, S., Blaricom, D.V. & Parsons, J. (1994) Hydrologic and wetland characteristics of a piedmont bottom in SC. *Water, Air and Soil Pollution*, **77**, 293–320.

Howarth, R.W., Billen, G., Swaney, D., Townsend, A., Jaworski, N., Lajtha, K., Downing, J.A., Elmgren, R., Caraco, N., Jordan, T., Berendse, F., Freney, J., Kudeyarov, V., Murdoch, P. & Zhu, Z.L. (1996) Regional nitrogen budgets and riverine N&P fluxes for the drainages to the North Atlantic Ocean: Natural and human influences. *Biogeochemistry*, **35**, 75-139.

Hupp, C. & Osterkamp, W. (1996) Riparian vegetation and fluvial geomorphic processes. *Geomorphology*, **14**, 277–295.

Keane, R.M. & Crawley, M.J. (2002) Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution*, **17**, 164–170.

King, J.R. & Tschinkel, W.R. (2008) Experimental evidence that human impacts drive fire ant invasions and ecological change. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 20339–20343.

Levine, J.M. (2001) Local interactions, dispersal, and native and exotic plant diversity along a California stream. *Oikos*, **95**, 397 – 408.

Lockaby, B.G. (2009) Floodplain ecosystems of the Southeast: linkages between

forests and people. *Wetlands*, **29**, 407–412.

Lockwood, J., Cassey, P. & Blackburn, T. (2005) The role of propagule pressure in explaining species invasions. *Trends in Ecology & Evolution*, **20**, 223–228.

Loewenstein, N. & Loewenstein, E. (2005) Non-native plants in the understory of riparian forests across a land use gradient in the Southeast. *Urban Ecosystems*, **8**, 79–91.

MacDougall, A.S. & Turkington, R. (2005) Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology*, **86**, 42–55.

McDonald, R. & Urban, D. (2006) Edge Effects on Species Composition and Exotic Species Abundance in the North Carolina Piedmont. *Biological Invasions*, **8**, 1049–1060.

McDonald, R.I., Motzkin, G. & Foster, D.R. (2008) Assessing the influence of historical factors, contemporary processes, and environmental conditions on the distribution of invasive species. *Journal of the Torrey Botanical Society*, **135**, 260–271.

McKinney, M. (2002) Urbanization, Biodiversity, and Conservation. *BioScience*, **52**, 883 – 890.

McKinney, M. (2008) Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosystems*, **11**, 161–176.

Merriam, R.W. (2003) The abundance, distribution and edge associations of six non-indigenous harmful plants across NC. *Journal of the Torrey Botanical Society*, **130**, 283–291.

Miller, J.H. (2003). *Nonnative invasive plants of southern forests: a field guide for identification and control.* Gen. Tech. Rep. SRS-62. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station.

Miller, J.H., Chambliss, E.B. & Oswalt, C.M. (2008) Maps of occupation and estimates of acres covered by nonnative invasive plants in southern forests using SRS FIA data posted on March 15, 2008. http://srsfia2.fs.fed.us/nonnative_invasive/Southern_Nonnative_Invasives.htm. Accessed on 1 December 2009.

Morris, L., Walck, J. & Hidayati, S. (2002) Growth and reproduction of the invasive Ligustrum sinense and native Forestiera ligustrina (Oleaceae): Implications for the invasion and persistence of a nonnative shrub. *International Journal of Plant Science*, **163**, 1001–1010.

National Climatic Data Center (NCDC). (2009) Palmer hydrological drought index for the northwest division of South Carolina. http://www7.ncdc.noaa.gov/CDO/CDODivisionalSelect.jsp . Accessed 15 December 2009.

Osland, M.J., Pahl, J.W. & Richardson, C.J. (2009) Native Bamboo [Arundinaria gigantea (Walter) Muhl., Poaceae] Establishment and Growth after the Removal of an Invasive Non-Native Shrub (Ligustrum sinense Lour., Oleaceae): Implications for Restoration. *Castanea*, **74**, 247–258.

Palumbi, S.R. (2001) Evolution - Humans as the world's greatest evolutionary force. *Science,* **293**, 1786-1790

Panetta, F. (2000) Fates of fruits and seeds of *Ligustrum lucidum* W.T.Ait. and *L. sinense* Lour. maintained under natural rainfall or irrigation. *Australian Journal of Botany*, **48**, 701–706.

Poff, N.L., Allan, J.D., Bain, M.B., Karr, J.R., Prestegaard, K.L., Richter, B.D., Sparks, R.E. & Stromberg, J.C. (1997) The natural flow regime. *BioScience*, **47**, 769–784.

Poff, N., Bledsoe, B. & Cuhaciyan, C. (2006) Hydrologic variation with land use across the contiguous United States: Geomorphic and ecological consequences for stream ecosystems. *Geomorphology*, **79**, 264–285.

Predick, K.I. & Turner, M.G. (2008) Landscape configuration and flood frequency

influence invasive shrubs in floodplain forests of the Wisconsin River (USA). *Journal of Ecology*, **96**, 91–102.

Schoonover, J.E., Lockaby, B. & Helms, B. (2006) Impacts of Land Cover on Stream Hydrology in the West Georgia Piedmont, USA. *Journal of Environmental Quality, **35**,* 2123–2131.

South Carolina Exotic Pest Plant Council (SC-EPPC). (2008) Invasive Plant List. http://www.se-eppc.org/southcarolina/. Accessed on 27, December 2009.

Strong, C., Brown, D. & Stouffer, P. (2005) Frugivory by Wintering Hermit Thrush In Louisiana. *Southeastern Naturalist*, **4**, 627–638.

Trimble, S.W. (1997) Contribution of stream channel erosion to sediment yield from an urbanizing watershed. *Science*, **278**, 1442–1444.

Trimble, S.W., Weirich, F. & Hoag, B. (1987) Reforestation and the reduction of water yield on the southern Piedmont since circa 1940. *Water Resources Research*, **23**, 425–437.

U.S. Department of Agriculture. (2009) The PLANTS Database. http://plants.usda.gov Accessed on 27 December 2009. National Plant Data Center, Baton Rouge, LA 70874-4490 USA.

U. S. Fish and Wildlife Service. 2009. Classification of Wetlands and Deepwater Habitats of the United States. http://www.fws.gov/wetlands/. U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C.

Vitousek, P.M., Mooney, H.A., Lubchenco, J. & Melillo, J.M. (1997) Human domination of Earth's ecosystems. *Science*, **277**, 494–499.

Von Holle, B. & Simberloff, D. (2005) Ecological resistance to biological invasion overwhelmed by propagule pressure. *Ecology*, **86**, 3212–3218.

Walsh, C.J., Roy, A.H., Feminella, J.W., Cottingham, P.D., Groffman, P.M. & Morgan, R.P. (2005) The urban stream syndrome: current knowledge and the

search for a cure. *Journal of the North American Benthological Society*, **24**, 706–723.

Walter, R.C. & Merritts, D.J. (2008) Natural Streams and the Legacy of Water Powered Mills. *Science*, **319**, 299 – 304.

Ward, R. W. (2002) Extent and dispersal rates of Chinese Privet (Ligustrum sinense) invasion on the upper Oconee River floodplain, north Georgia. *Southeastern Geographer*, **42**, 29– 48.

Weakley, A.S. (2008) *Flora of the Carolinas, Virginia, and Georgia, and Surrounding Areas*. http://www.herbarium.unc.edu/flora.htm. Accessed on 1 November 2009

Westoby, M., Dalby, J. & Adams-Acton, L. (1983) Fruit production by two species of privet, *Ligustrum sinense* Lour. and *L. lucidum* W.T. Ait., in Sydney. *Australian Weeds*, **2**, 1–3.

With, K.A. (2002) The landscape ecology of invasive spread. *Conservation Biology*, **16**, 1192–1203.

Zhang, X., Zwiers, F.W., Hegerl, G.C., Lambert, F.H., Gillett, N.P., Solomon, S., Stott, P.A. & Nozawa, T. (2007) Detection of human influence on twentieth-century precipitation trends. *Nature*, **448**, 461-465.